AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 3207, 60 pp., 27 figures, 9 tables October 23, 1997

The Blue and Green Whiptail Lizards (Squamata: Teiidae: *Cnemidophorus*) of the Peninsula de Paraguana, Venezuela: Systematics, Ecology, Descriptions of Two New Taxa, and Relationships to Whiptails of the Guianas

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ISSN 0003-0082 / Price $7.20

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ABSTRACT

Two color morphs of whiptail lizards (*Cnemidophorus*), one brilliant blue and one bright green, occur in distinctly different habitats on the Paraguana Peninsula, Venezuela. Multidisciplinary analyses (karyotypes, protein electrophoresis, color pattern, scalation, using univariate and multivariate statistical techniques) revealed that the blue and the green lizards represent two distinctively different diploid bisexual species. The green lizard is an undescribed species of *Cnemidophorus*, which also occurs in other areas of Falcon, Venezuela and on the Guajira Peninsula, Colombia, in open dune or desert scrub communities. Comparisons with known *C. lemniscatus* from the Guianan Region suggest that the blue lizard, which occurs in less open habitats such as tropical thorn woodland, is best treated as an undescribed subspecies of *C. lemniscatus*. Although its occurrence off the Paraguana Peninsula is suspected also, this remains to be documented.

Both new taxa are named and diagnosed. Color photographs and details of morphological and genetic variation for the new taxa are presented and correlated with data from *C. lemniscatus* of the Guianan Region. The new subspecies is compared with populations of *C. lemniscatus* from northern Venezuela and northeastern Colombia and with *Cnemidophorus l. gaigei* of Colombia, which is currently recognized as a synonym of *Cnemidophorus l. lemniscatus*. In addition, we discuss nomina dubia in the synonymy of *C. lemniscatus*, we describe and illustrate the types of *C. scutata* (a synonym of *C. l. lemniscatus*), we illustrate the lectotype of *C. lemniscatus*, and we present a table of taxonomic characters for identifying the valid taxa that are described and reviewed.

The relationships of both new taxa to the geographically nearest congener, *Cnemidophorus arubensis* of Aruba Island, which is only 30 km north of the Paraguana Peninsula, are discussed, but they remain obscure. A small population of lizards considered by previous workers to be *Cnemidophorus lemniscatus* in sympatry with *C. arubensis* at one locality on Aruba Island probably is the green species described here as new.

The two species of *Cnemidophorus* on the Paraguana Peninsula are mainly allopatric or narrowly parapatric in their microgeographic distribution but sympatric at a few localities

with disturbed habitats. They do not appear to interbreed and are allotopic in areas of sympatry. These taxa differ from each other in habitat preferences and diet (the green taxon is primarily herbivorous), and they are similar in reproductive biology.

RESUMEN

Para muchas áreas del neotrópico falta información sobre la taxonomía, ecología e historia natural de los lagartos indígenas, la cual es fundamental para poder entender la historia de la diferenciación y el significado de las distribuciones actuales y su diversidad. La árida región de tierra baja del noroeste de Venezuela es uno de esos tipos de zonas, de modo que uno de nosotros (ALM) comenzó el estudio de la ecología y diversidad de la herpetofauna de la península de Paraguaná en 1989.

Las observaciones de los lagartos (*Cnemidophorus*) de allí, reveló una relación sorprendente entre el colorido y la ecología. Se daban dos morfos distintos de color en hábitats diferentes. Un morfo incluía lagartos de un azul brillante, el otro, lagartos de un verde brillante. Sin embargo, se pensaba que solamente una de las especies, el *Cnemidophorus lemniscatus* se daba en esta área de Venezuela. Estas especies y los congéneres de la región de Guyana (al norte del Río Amazonas y al este del Orinoco y del Río Negro) descritos recientemente, han sido considerados mas bien generales en lo que al hábitat se refiere.

Análisis multidisciplinarios (cariotipos, electroforesis de proteínas, colorido y escamación, usando técnicas estadísticas univariadas y multivariadas) revelaron que los lagartos azules y lagartos verdes de la península de Paraguaná son dos especies diploides y bisexuales claramente distintas. El lagarto verde es una especie de *Cnemidophorus* no descrita, que se da en otras áreas de Falcón, en Venezuela y en la península de Guajira, en Colombia. Las comparaciones con la conocida *C. lemniscatus* de la región de Guyana sugieren que el lagarto azul es tratado en la actualidad como una subespecie no descrita de *C. lemniscatus*. Aunque se sospecha su presencia fuera de la península de Paraguaná, se esperan datos exactos sobre la coloración de los lagartos que viven en los lugares relevantes.

Ambas formas han sido nombradas y diagnosticadas aquí. Las fotos en color y los detalles de la variación morfológica y genética para las nuevas formas se muestran y se correlacionan con datos de *C. lemniscatus* de la región de Guyana. La nueva subespecie se compara con poblaciones de *C. lemniscatus* del norte de Venezuela y del noreste de Colombia y con *Cnemidophorus l. gaigei* de Colombia, actualmente reconocida como sinónimo de *Cnemidophorus l. lemniscatus*. Además, lo tratamos nomina dubia en la sinonimia; describimos los tipos de *C. scutata* (un sinónimo de *C. l. lemniscatus*), ilustramos el lectotipo de *C. lemniscatus* y presentamos una tabla de caracteres taxonómicos para identificar los taxa válidos, descritos y revisados.

La relación de ambos taxa nuevos con el congénere más cercano geográficamente, el *Cnemidophorus arubensis* de la isla de Aruba, que está situada solamente a 30 km al norte de la península de Paraguaná, es poco clara. Se precisarán datos cariotípicos y otros datos genéticos de este último para poder resolverlo. El aislamiento de *C. arubensis* se trata en relación con la paleografía de Aruba y de la península de Paraguaná durante el último máximum glaciar. Una pequeña población de lagartos que investigadores anteriores consideraron que fuera *Cnemidophorus lemniscatus* en simpatría con *C. arubensis* en una localidad de la isla de Aruba, es probablemente la especie verde que se describe aquí como nueva.

El *Cnemidophorus* verde de la península de Paraguaná se da en hábitats abiertos con vegetación baja, tal como dunas de arena o matorrales de rastrojo. Es un herbívoro facultativo como otros congéneres próximos de la península, una adaptación que quizás se desarrolló como respuesta al severo medioambiente con reservas de comida impredecibles. El *Cnemidophorus* azul se asocia con hábitats más sombreados con vegetación más alta y espesa, tal como el matorral espinoso tropical o comunidades de bosques tropicales muy secos, y es carnívoro. Es posible que su distribución geográfica esté fragmentada y que fuera más extensa durante el último máximum glaciar debido a una mayor aridez y a comunidades florales secas más extensas. Ambos hábitats difieren del de *C. lemniscatus* oriental que se da típicamente en las sabanas y a su alrededor, y en otras áreas abiertas en climas con humedad generalmente superior a la del noroeste de las tierras bajas venezolanas.

El colorido del lagarto verde y del azul de la península de Paraguaná puede que se deba a adaptaciones crípticas a hábitats abiertos y más sombreados, respectivamente. Estas dos especies son mayormente alopátricas o parapátricas en su distribución microgeográfica en la península y simpátricas en unos cuantos lugares con hábitats dis-

turbados. No parece que se crucen y son alotópicas en zonas de simpatría. Las características estructurales de vegetación y el grado de apertura del hábitat parecen ser factores importantes en la división del hábitat.

Ambas especies de la península de Paraguaná, al parecer, tienen una nidada normal de dos huevos y la madurez reproductiva en las hembras tiene lugar cuando tienen una longitud corporal de unos 60 mm, aunque se precisan más datos para las hembras del taxón azul. Muestran dimorfismo sexual en el tamaño corporal, longitud de la cabeza y en varios rasgos de la escamación y del colorido. Aunque las hembras adultas de cada uno son dicromáticas y puede darse que tengan rayas o colorido como el de los machos adultos.

INTRODUCTION

Recent discoveries on the evolution and diversity of teiid lizards (sensu lato, including the "Gymnophthalmidae") of northern South America have been exciting and provocative with respect to understanding Neotropical diversity and its evolution. A species ancestral to a parthenogen of hybrid origin was predicted to exist on the basis of karyological and electrophoretic evidence gathered in the laboratory (Cole et al., 1989, 1990) and subsequently the taxon was found in nature (Cole et al., 1993; Cole, 1994). The traditional concept that *Cnemidophorus* was represented in northern South America by only one species, *Cnemidophorus lemniscatus* (Linnaeus), underestimated the tropical richness in this genus. Recently, new taxa of both unisexual and bisexual species have been described (McCrystal and Dixon, 1987; Cole and Dessauer, 1993), some first detected through genetic analyses (Dessauer and Cole, 1989; Sites et al., 1990), and we are aware of the existence of others.

The origin of most tropical species of lizards was probably by adaptation to local environments in isolation through allopatric speciation, although some taxa are of instantaneous hybrid origin (e.g., Dessauer and Cole, 1989; Cole and Dessauer, 1993). There is evidence supporting models of differentiation in refugia during the Quaternary in response to climatic vicissitudes and correlated forest and savanna contraction and expansion (Haffer, 1987). However, as more detailed ecological knowledge is gained, there are indications that these models may be overly simple, which tends to obscure the complexity of tropical communities and ecosystems, both within present and historical contexts (for a review, see Avila-Pires, 1995:599–615). Vitt (1996) has shown, for example, that the lizard, *Norops* (or *Anolis*) *chrysolepis*, a species previously used in studies of South American refugia (Vanzolini and Williams, 1970) is ecologically more complex than previously conceived. Vitt and Zani (1996) also underscored the insufficiency of ecological and basic natural history information for many tropical lizards; models that connect historical differentiation to changing regimes of selection are tentative at best if relevant ecological knowledge is lacking.

In addition, little is known of the alpha-level taxonomic diversity in many areas of the tropics, for example, in the Caribbean arid areas of northwestern Venezuela and northeastern Colombia. The rather stark, open landscapes of these dry areas may initially suggest biotic simplicity but they are ecologically complex with numerous different biotic communities depending on local topography and microclimates (Rivero-Blanco and Dixon, 1979; Sarmiento, 1976). Such communities likely experienced dynamic changes during Quaternary climatic vicissitudes, as did the savannas and forests of northern South America (Haffer, 1987). Lists of the herpetofauna of this area are mostly incomplete and dated (e.g., Marcuzzi, 1950, 1954; Ruthven, 1922), and there is even less information on its ecology.

In 1989 one of us (ALM) began faunistic and ecological studies on the Peninsula de Paraguana of northwestern Venezuela and continued this work intermittently for the following four years. Since very little previous research was done on the peninsula—probably in no small part due to the inhospitable climate with extremely high temperatures and strong, dry winds creating blast furnace-like conditions—these studies resulted in the addition of several species to the peninsular, and in some cases, Venezuelan fauna (e.g., Mijares-Urrutia et al., 1995), the discovery

of a diminutive, secretive gecko new to science (Markezich and Taphorn, 1994), and recommendations to the Venezuelan government concerning conservation of the peninsular biotic diversity. Yet, one of the most interesting discoveries concerned lizards that are among the most conspicuous animals on the peninsula—the whiptails of the genus *Cnemidophorus*—as reported here.

From the onset of the fieldwork, two striking color pattern morphs were apparent among the *Cnemidophorus*—a brilliant blue one and a bright green one (figs. 13 and 14). *Cnemidophorus lemniscatus* was the only species of this genus previously recorded from the peninsula (Lammeree, 1970; Marcuzzi, 1950, 1954), and it has a wide range of variation in color pattern (Beebe, 1945). As studies progressed, it became apparent that the two color forms have different microgeographic distributions that are highly correlated with local ecological factors. The blue whiptails live in the more shaded thorn woodland communities, and the green ones in the open sands of the dunelands and deserts. We now know that these forms are allopatric or narrowly parapatric at most localities and sympatric in a few, with no evidence of hybridization. These observations suggested that these animals represent two ecologically distinct species. Initially this was rather surprising as species of the *C. lemniscatus* complex have usually been reported as habitat generalists occurring in open, sometimes disturbed, areas with low vegetation (Beebe, 1945; Vanzolini, 1970; Hoogmoed, 1973; McCrystal and Dixon, 1987; Vitt and de Carvalho, 1995). Magnusson et al. (1986), however, reported more specific habitat selection with respect to vegetative cover and soil type by *C. lemniscatus* in a savanna in northern Brazil. Previous work on the systematics and ecology of whiptails of this complex have not indicated local interspecific associations with different kinds of vegetation, and narrowly parapatric or allopatric and ecologically distinct species of the *C. lemniscatus* complex have never been documented.

For the present report we compared ecology, morphology, karyotypes, and biochemical genetics of these colorful animals with each other and with genetically confirmed samples of *C. lemniscatus* from Brazil, Suriname, Guyana, and eastern Venezuela, following Cole and Dessauer (1993). We address the following questions: (1) Are the green and the blue *Cnemidophorus* from the Paraguana Peninsula two different species, and if so what are their basic morphological, genetic, ecological, distributional, and behavioral characters? (2) Is one of the species from the Paraguana Peninsula a local population of *C. lemniscatus*? (3) Is one of the species from the Paraguana Peninsula a local population of *C. gramivagus*? (4) Is one (or are both) of these a new species to be named and described? (5) Is one of these the second ancestor of the recently described, unisexual *C. cryptus* (diploid) and *C. pseudolemniscatus* (triploid) of the Guianan Region? The comparisons include samples recently collected in Guyana by one of us (CJC) and Carol R. Townsend, confirming that populations on the Rupununi Savanna are properly referred to *C. lemniscatus* also. Finally, in the context of describing two new taxa, we review the lectotype of *C. lemniscatus*, the type specimens of one of its synonyms, *C. scutata* Gray, and some nomina dubia.

ACKNOWLEDGMENTS

Fieldwork by ALM in Venezuela was made possible by the PROFAUNA division of the Venezuelan Ministerio del Ambiente y de los Recursos Naturales Renovables (MARNR), Caracas, who kindly issued collecting permits and furnished other help. Numerous people from the Paraguana Peninsula offered essential assistance with this project. Dario Bracho of Pueblo Nuevo furnished valuable information and maps of the Monte Cano area. Esteban Cuauro and his family and Tomas Lugo, both of San Jose de Cocodite, were both friends and guides, undaunted by the spines, heat, and cascabels. Edgar Wefer of Adicora collected several specimens and he and his family generously provided critical logistical support throughout much of the project. Madelynn J. Markezich helped with the collection of specimens and observations in the field, and she and Matthew L. Markezich helped and supported ALM throughout the course of the project.

Special thanks go to a friend and colleague, Donald C. Taphorn, Director of the Museo de Ciencias Naturales, UNELLEZ, Guanare, Estado Portuguesa for the support, help, and logistical field assistance he provided. Also the assistance of the staff at the museum and others at UNELLEZ is greatly appreciated.

Refer to Cole and Dessauer (1993) and Cole et al. (1995) for detailed acknowledgments of those who have contributed to our research in Guyana, Suriname, and Venezuela for over 15 years. This paper has benefited from the assistance and cooperation of all those people. In particular, in obtaining the samples of *C. lemniscatus* found in 1992 in the vicinity of Yupukari on the Rupununi Savanna, Guyana, on which we report in detail here for the first time, we were assisted by the following: Karen Pilgrim, Wildlife Services Division, Department of Agriculture, Guyana; the Biological Diversity of the Guianas Program (BDGP), coordinated in 1992 in Guyana by Deputy Vice-Chancellor Malcolm Rodrigues and Dean Indarjit Ramdass of the University of Guyana (UG), Turkeyen Campus, Georgetown; Mike Tamessar, UG; Vicki A. Funk and Carol Kelloff, coordinating the BDGP in North America through the Department of Botany, National Museum of Natural History, USA.; Bruce Hoffman, BDGP; Malcolm Chan-A-Sue (Torong Guyana); Walter Lachman (Guyana National Dairy Development Programme); Diane McTurk (Karanambo, Guyana); the people of Karanambo and Yupukari; the "Ambassador of Bourda," Mohammed Ameer (BDGP); and Carol R. Townsend, American Museum of Natural History (AMNH).

The following individuals lent preserved specimens and assisted in many other ways with this project: E. N. Arnold and C. J. McCarthy of the Natural History Museum, London (BMNH); Harold Voris and Alan Resetar of the Field Museum of Natural History (FMNH); John Cadle, Ernest Williams, and Jose Rosado of the Museum of Comparative Zoology (MCZ), Harvard University; Arnold Kluge of the Museum of Zoology, University of Michigan (UMMZ); George Zug of the United States National Museum (USNM); and Lars Wallin of the Zoological Museum, Uppsala University, Sweden (ZMUU).

Ernest E. Williams is one of the few North American herpetologists who has worked on the Paraguana Peninsula and discussions with him were invaluable. In addition, Joseph J. Schall provided important insights into the ecology of insular *Cnemidophorus* that occur near the Paraguana Peninsula.

We wish to thank SPSS, Inc., Chicago, Illinois, for providing their statistical software packages, SYSTAT (for DOS and Windows), to ALM; these were used to analyze much of the data.

Specimens were karyotyped and tissue samples were processed while CJC was working at the Southwestern Research Station of the AMNH, Portal, Arizona. Wade C. Sherbrooke, Timothy Almaguer, and Carol R. Townsend assisted significantly in this work. Wayne A. Riddle of Illinois State University helped with several figures, and C. Lucas-Murillo prepared the Spanish abstract, which was proofed by Victor Pacheco. We also thank T. C. S. de Avila-Pires (Museu Paraense Emilio Goeldi, Belem, and National Museum of Natural History, Leiden), Darrel R. Frost (AMNH), and Marinus S. Hoogmoed (National Museum of Natural History, Leiden) for very helpful reviews of the manuscript. This is publication number 31 in the BDGP series, "Biological Diversity of the Guianas."

METHODS

The specimens examined are listed in the appendix together with the kind of data taken from each.

FIELDWORK

Most specimens from the Paraguana Peninsula and associated ecological data were collected by one of us (ALM) during the following periods: July—August of 1989, 1991, 1992, 1993, and November–December, 1990. Body (cloacal) temperatures of lizards were recorded with a hand-held Omega microprocessor thermometer with copper thermocouples (model HH23); data were recorded only for lizards that were captured or shot immediately upon being found. Ambient temperature was recorded 5 cm above the ground (shaded).

KARYOTYPES

Chromosomes were prepared from femoral bone marrow and studied as described for other teiid lizards (Cole, 1979). We examined chromosomes of 30 mitotic cells from six lizards, three specimens each of the blue and the green forms from the Paraguana Peninsula.

BIOCHEMICAL GENETICS

Samples of fresh tissues (liver, heart, skeletal muscle, kidneys, stomach, small intestine, plasma, and blood cells) were frozen in liquid nitrogen and stored in ultra-cold freezers prior to use, following traditional procedures (e.g., Dessauer et al., 1996).

Electrophoresis of tissue proteins of 32 specimens of *Cnemidophorus* from Venezuela and Guyana, additional to those reported by Cole and Dessauer (1993), was conducted as described in detail for other teiid lizards (Dessauer and Cole, 1991). Table 1 here lists the 39 presumptive gene loci examined, Enzyme Commission numbers, abbreviations, and the tissues and buffers used. Table 2 presents cross-correlations between these new data and those reported by Cole and Dessauer (1993) for other populations of *Cnemidophorus* in northern South America (Venezuela, Brazil, and Suriname).

EXTERNAL MORPHOLOGY

For most characters of scalation and size, we followed Wright and Lowe (1967), Cole et al. (1988), and Cole and Dessauer (1993). The characters used and their abbreviations (in parentheses) are: shape of anal spur of males (ASPUR, see below); total number (sum of left and right counts) of circumorbital scales (COS); shape of posterior margin of central enlarged preanal shield (CPAS, see below); total number of fourth finger lamellae (FLS); total number of femoral pores (FP); number of gular scales (GUL); proportion of head length to snout-vent length (HL/SVL), for which head length was measured from tip of snout to palpable posterior end of upper and lower jaw articulation; number of scales between medial femoral pores (IFS); total number of interlabial scales (ILS); position of nostril with respect to nasal suture (NAS, see below); number of granular scales around midbody (axilla–groin) (SAB); number of granules between paravertebral light stripes (SPV), at midbody; proportion of SPV to SAB (SPV/SAB); snout-vent length (SVL); total length (TOTL); proportion of SVL to TOTL (SVL/TOTL), for specimens with complete, unregenerated tails (TL); and total number of fourth toe lamellae (TLS).

Shape of the anal spur in males was assigned to one of three states as determined by reference to figure 7 of Cole and Dessauer (1993: 16): 1, a rather evenly tapered spur with a narrow base such as found in *Cnemidophorus gramivagus*; 2, a shape between states 1 and 3, with a narrower base than 3 but wider than 1; and 3, a very broad based spur tapering abruptly to a point near the apex, typical of *C. lemniscatus*. Three character states recorded for the position of the nostril with respect to the nasal suture were: 1, almost entire nostril anterior to suture, with the latter essentially forming the posterior border of the nostril; 2, more than half of the nostril anterior to the suture; and 3, nostril centered with respect to the suture.

The preanal shield arrangement was Type I (Lowe and Wright, 1964) in almost all specimens examined and consequently was of little taxonomic importance. However, the posterior angle of the enlarged, central preanal shield (CPAS) was found to be a valuable character and was assigned to one of six categories: 1, strongly acute, 60° or less; 2, acute, between 60 and 90°; 3, orthogonal, 90°; 4, obtuse, between 90 and 120°; 5, strongly obtuse, greater than 120°; and 6, central shield divided into two subequal shields with the posterior edge of the two approximately 180°. This character was usually evaluated by visual comparison to a scale of angles that was made for the purpose; where difficult to evaluate by this procedure, trigonometry was employed.

Color pattern groups might be designated B, G, or L; these letters refer, respectively, to the blue animals from the Paraguana Peninsula, the green animals from the Peninsula, and the specimens of *Cnemidophorus lemniscatus* from Guyana, Suriname, and eastern Venezuela.

Sex of most specimens was determined by

TABLE 1
Presumptive Structural Gene Loci Examined in *Cnemidophorus*

Locus	EC no.	Abbrev.[a]	Tissue[b]	Buffer[c]
Oxidoreductases				
Glycerol-3-phosphate dehydrogenase	1.1.1.8	G3PDH	M	TC8
L-Iditol dehydrogenase	1.1.1.14	IDDH	K	TC8
L-Lactate dehydrogenase	1.1.1.27	LDH-1	K	TC8
		LDH-2	M	TC8
Malate dehydrogenase	1.1.1.37	sMDH	M	PC6[d]
		mMDH	M	TC8
Malate enzyme	1.1.1.40	sMDHP	M	PC6; TC8
		mMDHP	M	PC6; TC8
Isocitrate dehydrogenase	1.1.1.42	sIDH	K	TC8
		mIDH	M	TC8
Phosphogluconate dehydrogenase	1.1.1.44	PGDH	K	TC8
Glucose-6-phosphate dehydrogenase	1.1.1.49	G6PDH	K	TC8
Superoxide dismutase	1.15.1.1	SOD[e]	L	TC8
Transferases				
Aspartate aminotransferase	2.6.1.1	sAAT	M	TC8
		mAAT	M	TC8
Creatine kinase	2.7.3.2	CK-1	K	TC8
		CK-2	K	TC8
Adenylate kinase	2.7.4.3	AK	M	TC8
Hydrolases				
Esterase D	3.1.1-	ESTD[f]	K	TC8
Esterase (nonspecific)		EST[g]	M	TC8
Alkaline phosphatase	3.1.3.1	ALP	L	TC8
Acid phosphatase	3.1.3.2	ACP[h]	M	PC6
B-galactosidase	3.2.1.23	BGAL[i]	R	PC6
Alpha-mannosidase	3.2.1.24	aMAN[j]	R	TC8
Peptidases	3.4.-.-	PEPA[k]	M	TC8
		PEPB[l]	M	TC8
		PEPE[l]	M	TC8
Proline dipeptidase	3.4.13.9	PEPD[m]	R	TC8
Adenosine deaminase	3.5.4.4	ADA	R	PC6
Lyases				
Aconitate hydratase	4.2.1.3	sACOH	L	TC8
		mACOH	L	TC8
Isomerases				
Mannose-6-phosphate isomerase	5.3.1.8	MPI	K	PC6; TC8
Glucose-6-phosphate isomerase	5.3.1.9	GPI	K,M	PC6; TC8
Phosphoglucomutase	5.4.2.2	PGM	M	TC8
Nonenzymic proteins				
Albumin		ALB	P	V8.6
Transferrin		TF	P	V8.6
Hemoglobin		HB-1	R	PC6
		HB-2	R	PC6
Myoglobin		MB	M	TC8

[a] Based largely on Murphy et al. (1996); s = cytosolic enzyme; m = mitochondrial enzyme. For multilocus systems, loci are numbered in order of decreasing anodal migration of their polypeptide products.

[b] Tissue in which enzyme was scored most effectively: H = heart; K = kidney; L = liver; M = skeletal muscle; P = plasma; R = erythrocytes.

[c] Components followed by pH; T = TRIS; C = citrate; P = phosphate; V = veronal (barbituric acid).

[d] No variation was observed at sMDH at pH8.

[e] The sSOD and mSOD could not be distinguished in these lizards.

[f] Substrate 4-methylumbelliferyl acetate; inactive with alpha-napthyl esters.

dissection, but for some we relied on presence (male) or absence (female) of conspicuous anal spurs.

Color notes and photographs were taken in life for specimens we collected. The animals had from 2 to 10 light stripes evident at midbody (i.e., mid axilla-groin), alternating with dark stripes. The number of light stripes varies with age and sex (see below). There is no standard terminology in wide usage for reference to these stripes in *Cnemidophorus lemniscatus*; so we explain our usage here. In a lizard with a full complement of light stripes at midbody (usually 9 or 10, see below), the sequence of light and dark stripes of taxonomic importance, on either the right or left side of the body, beginning in the vertebral region and ending on the lower lateral side, would be (fig. 1): vertebral light stripe (VLS), paravertebral dark stripe (PDS), paravertebral light stripe (PLS), dorsolateral dark stripe (DDS), first lateral light stripe (1LL), second lateral light stripe (2LL), and third lateral light stripe (3LL). If the vertebral light stripe is absent, the two paravertebral dark stripes become continuous medially and could be called the vertebral dark strip, or VDS.

The vertebral light stripe was recorded as single, absent, or split; when split or absent, a specimen would have an even number of light stripes and when single, an odd number. A split VLS was manifest in various ways: split anteriorly on the neck, merging there, and continuing posteriorly to the base of the tail as one (see fig. 10 of Cole and Dessauer, 1993); split anteriorly and merging somewhere between the axilla and groin (fig. 11 B, C of Cole and Dessauer, 1993); split all along the body to the base of the tail (fig. 1B here). In the first two cases, the continued single stripe often displayed irregular edges. All of these conditions were recorded as split in the present study.

In some specimens the vertebral stripe was split to the extent that at first glance it was unclear whether the lizard lacked the vertebral stripe or had a fully split one, which masqueraded as paravertebral light stripes. In such cases, the question of homology was resolved by counting light stripes (or their remains as spots on larger specimens) from the level of the upper edge of the tympanum upward. In all instances, if the light stripe that passes immediately over the upper edge of the ear is counted as number one, the vertebral stripe is number four, whether the vertebral stripe is split widely or not at all. In cases where stripes and/or spots above the tympanum are difficult to determine, a vertebral light stripe can be ascertained as split if there is a narrow dark vertebral stripe, normally of similar color and shade as the paravertebral dark stripes; three rather than two dark dorsal stripes are apparent at midbody (fig. 1B). In some specimens in which the vertebral light stripe is widely split, a rather faint additional light stripe occurs in the middle of what otherwise would be the dark vertebral area (for example, fig. 25).

For specimens with a split vertebral light stripe, the number of granules between the paravertebral light stripes was counted between the true paravertebral light stripes as defined above, not just within the dark strip between the split halves of the vertebral light stripe.

Rationale for statistical analyses followed Snedecor and Cochran (1980), Sokal and Rohlf (1981), or Wilkinson et al. (1996). Analyses were performed with various program modules in version 5.01 and 6.0 of SYSTAT for DOS and version 6.0 of SYSTAT for Windows (SPSS, Chicago, Illinois).

←

[g] Substrates 4-methylumbelliferyl acetate or alpha-napthyl esters.

[h] Substrate 4-methylumbelliferyl phosphate.

[i] Substrate 4-methylumbelliferyl-beta-D-galactoside.

[j] Substrate 4-methylumbelliferyl-alpha-D-mannopyranoside.

[k] Substrate phenylalanyl.leucine.

[l] Substrate leucyl. glycyl.glycine.

[m] Substrate phenylalanyl.proline.

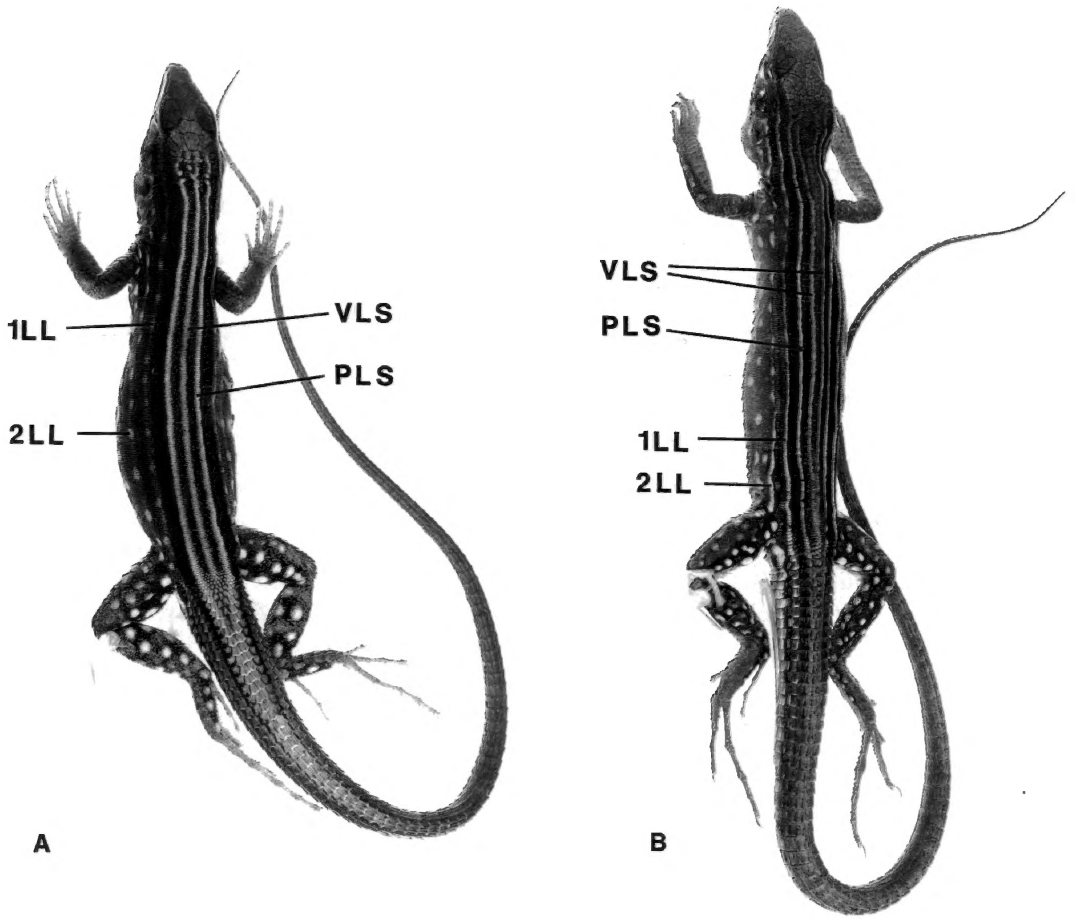

Fig. 1. Patterns of dorsal stripes in *Cnemidophorus* as discussed here. **A.** The blue lizard (named *Cnemidophorus l. splendidus* below), paratype, AMNH 142589, from the Paraguana Peninsula, with a single vertebral light stripe; 1 LL and 2 LL are represented by a collinear series of spots that are connected by very thin lines. **B.** *Cnemidophorus l. lemniscatus*, AMNH 133299, from Suriname, with a split vertebral stripe. Abbreviations: VLS, vertebral light stripe (which is bordered laterally by the paravertebral dark stripe); PLS, paravertebral light stripe (which is bordered laterally by the dorsolateral dark stripe); 1 LL, first lateral light stripe; 2 LL, second lateral light stripe.

Numerical subscripts following symbols for statistical tests of significance (for example, t_{42}) indicate the number of degrees of freedom associated with the particular test. All t-test results are based on two-tailed tests with pooled variances.

In univariate analyses of 14 variables involving scalation and size between sexes and between the blue lizards, the green lizards, and *C. lemniscatus*, we performed a Bartlett's Test for homogeneity of variances before subsequent tests for differences among means. Several variables that exhibited heteroscadasticity were transformed by using either natural logarithms (COS, IFS, ILS, SPV, TLS, SAB, SVL, FP) or arcsine transformations where proportions were involved (SPV/SAB, SVL/TOTL, HL/SVL). Subsequent tests for sexual dimorphism and differences among means of these variables involved an analysis of variance between all color and sex groups (six groups) followed by a Tukey HSD which yielded all possible intergroup comparisons. For four variables with heterogeneous variances that transformations did not stabilize (FLS, SVL, TOTL, and HL/SVL) Mann-Whitney *U* tests were used on original values. In the table reporting sta-

tistics of dispersion, the original measured values for all variables are reported, rather than the antilog back-transformed values.

In other univariate analyses involving meristic values, such as number of individuals associated with various character states, Mann-Whitney *U* tests were used to evaluate differences; this particularly applied to ASPUR, NAS, and CPAS and several variables related to color pattern.

The HL/SVL ratio was calculated only for adults ≥ 60 mm SVL; this is the approximate size at which reproductive maturity begins (see Results and Discussion). In order to eliminate intergroup differences related to body size differences, the relationship between log (natural log) head length and log SVL was examined in blue lizards, green lizards, and *C. lemniscatus* with an analysis of covariance (ANCOVA) using log SVL as the covariate. Slope parallelism, a requirement of ANCOVA, was determined by examination of the interaction term in a two-way ANOVA involving color and log SVL between the three groups. A post hoc Bonferroni test was used to examine pairwise differences among adjusted means.

Two principal components analyses were performed on log-transformed variables utilizing an extracted correlation matrix. Proportions were excluded from this analysis; continuous variables and meristic variables where a natural progression of states could be established (e.g., CPAS) were used. Values reported are for original, unrotated solutions.

RESULTS AND DISCUSSION

Evidence from Karyotypes

We compared karyotypes of the following samples and specimens of *Cnemidophorus* from the Paraguana Peninsula, Venezuela: blue lizards (two males, one female; 15 cells); and green lizards (two males, one female; 15 cells)—see Appendix for specimens examined.

All lizards examined had the same karyotype (fig. 2). Each had a diploid number of 50 chromosomes, with the largest pair submetacentric to subtelocentric (having a dot-like satellite set off by a nearly terminal secondary constriction on the long arm), 24 somewhat smaller telocentric macrochromosomes (apparently 12 pairs), and 24 microchromosomes (12 pairs). Morphology of the microchromosomes is difficult to resolve with standard compound microscopy, but usually two and up to four appear biarmed in the clearest cells. No heteromorphic sex chromosomes were observed.

No karyotypic differences were observed between the green and the blue *Cnemidophorus*. Furthermore, their karyotype appears identical to that of *Cnemidophorus lemniscatus* as this species is currently understood (specimens referred to cytotype D by Peccinini-Seale and Frota-Pessoa, 1974; Dessauer and Cole, 1989; Sites et al., 1990; Cole and Dessauer, 1993). Consequently, karyotypes do not help us sort out the species in this instance; they only demonstrate that whatever the species are, they share the same karyotype with the bisexual *C. lemniscatus* of the Guianan Region. Although the karyotypic data would be consistent with referring all of these lizards to *C. lemniscatus*, other genetic, morphological, and distributional data are not (see below).

Evidence from Biochemical Genetics

Proteins encoded by 39 presumptive structural gene loci (table 1) were analyzed by electrophoresis for the following *Cnemidophorus*: 13 green lizards from the Paraguana Peninsula, Venezuela (allowing detection of allelic frequency variation down to the level of 1/26 or 4%); 8 blue specimens from the Paraguana Peninsula, Venezuela (allelic variation to 6%); 10 specimens from Yupukari (Rupununi Savanna), Guyana (allelic variation to 5%); and samples of *Cnemidophorus lemniscatus* and *Cnemidophorus cryptus* reported by Cole and Dessauer (1993) were included to provide cross-correlations with their published data. Our results are presented in table 2 and figures 3–5.

Table 2 presents our comparative electrophoretic results, keyed to figure 3 showing sample localities, as follows: the GREEN and the BLUE lizards (table 2) are both from the Paraguana Peninsula (fig. 3, P); LEMG (table 2) are *C. lemniscatus* from Yupukari, Guyana (fig. 3, O); LEMV (table 2) are *C. lemniscatus* from San Ignacio de Yuruani, Venezuela (fig. 3, D in eastern Venezuela); CRY (table 2) are *C. cryptus* from Icabaru,

TABLE 2

Alleles[a] or Genotypes[b] at 39 Presumptive Structural Gene Loci[c] in Samples[d] of *Cnemidophorus* from South America

Locus[c]	GREEN	BLUE	LEMG	LEMV	CRY	OTHER[e]
IDDH	b	b	b	b,a[f]	bb	same
LDH-1	b	b,a[g]	b	b	bb	b = w
sMDH	a,b[i]	a	a,b[g]	a	aa	a = w
mMDHP	a	b,c[h]	b	b	bb	—
mIDH	d	c	a	a	ab	same
SOD[j]	b,a[i]	b	b,a[g]	b	bb	b = w
sAAT	a	b	b	b	ab	same
ESTD	a	a	a	b[k]	aa	same
EST[l]	B	A	—	—	—	—
ACP	b,a[m]	a	a,b[f]	a	aa	a = w
BGAL	a,b[m]	a	b,a[h]	a	—	—
PEPA	a	b	b	b	ab	same
PEPB	b,a[i]	b,a[g]	a	a	ab	same
PEPD	b,a[n],c[i]	a,c[g]	a	a	aa	—
ADA	b	d,c,e,f[o]	e,d[n]	d	ad	a = a; d = b
sACOH	a	b	b	b	bb	b = b
MPI	c,b[n],a[g]	c,a[h]	c	c	cc	c = b
GPI	a	b	b,a[g]	b[p]	bb	b = b
ALB	b,a[h]	a,b[h]	a,b[f]	b[p]	—	—
TF	a,b[n]	a,b[g]	b	b	bb	b = w

[a] Alleles are designated in alphabetical sequence in order of decreasing anodal migration. Commas separate alternative alleles at a specific locus for bisexual species; alleles at polymorphic loci are listed in order of decreasing frequency.

[b] Polymorphisms were fixed in the unisexual CRY so genotypes are given for that species.

[c] See table 1. Gene products for the following 19 loci had identical patterns in all lizards tested for this paper, consistent with Cole and Dessauer (1993) except as noted: G3PDH, LDH-2, mMDH, sMDHP (see Cole and Dessauer, 1993, for a discussion of alternative alleles in Brazilian *Cnemidophorus*), sIDH, PGDH, G6PDH (not tested by Cole and Dessauer, 1993), mAAT, CK-1, CK-2, AK, ALP (not tested by Cole and Dessauer, 1993), aMAN (not tested by Cole and Dessauer, 1993), PEPE (not tested by Cole and Dessauer, 1993), mACOH (see Cole and Dessauer, 1993, for a discussion of alternative alleles in *Cnemidophorus* from Suriname), PGM (not tested by Cole and Dessauer, 1993), HB-1, HB-2 (the HB loci were not tested by Cole and Dessauer, 1993), and MB.

[d] GREEN = *Cnemidophorus* from the Paraguana Peninsula, Venezuela, characterized by a green dorsal coloration (named *C. arenivagus* below; N = 13 examined); BLUE = *Cnemidophorus* from the Paraguana Peninsula characterized by a brilliant blue dorsal coloration (named *Cnemidophorus lemniscatus splendidus* below; N = 8); LEMG = *Cnemidophorus lemniscatus* from Yupukari, Guyana (N = 10); LEMV = *Cnemidophorus lemniscatus* from San Ignacio de Yuruani, Venezuela, the same specimens from this site as reported by Cole and Dessauer (1993; N = 7; AMNH number of 134227 was used for detailed cross-correlations); CRY = *Cnemidophorus cryptus* from Icabaru, Venezuela, the same specimens from this site as reported by Cole and Dessauer (1993; N = 5, with AMNH number 135090 added and used for detailed cross-correlations). See Appendix for specimens examined.

[e] Alleles listed for GREEN, BLUE, LEMG, LEMV, and CRY are designated as recorded from the new gels analyzed for this paper. The last column (OTHER) compares these alleles (first given) with those reported previously (second given) for additional South American *Cnemidophorus* by Cole and Dessauer (1993). A w ("wild type") means an allele that was invariant in the specimens examined by Cole and Dessauer (1993).

[f] Frequency = 0.21 to 0.30.

[g] Frequency = 0.05 to 0.10.

[h] Frequency = 0.11 to 0.20.

[i] Frequency = 0.00 to 0.05.

[j] We could not distinguish between sSOD and mSOD in these lizards.

[k] Frequency of the b allele varies geographically in *C. lemniscatus* (see Cole and Dessauer, 1993). The a allele occurs in Suriname and Brazil also.

[l] Although the genetics of this particular esterase are not worked out, phenotypic scoring revealed a consistent difference between the green and the blue lizards from the Paraguana Peninsula.

Venezuela (fig. 3, C in eastern Venezuela); and OTHER (table 2) correlates the alleles as found on the gels run for this paper with those reported by Cole and Dessauer (1993) for the Guianan Region. Figures 4 and 5 are examples of gels run for this paper.

Are the Green and the Blue *Cnemidophorus* from the Paraguana Peninsula Two Different Species?

For eight of the 39 loci analyzed (20%; table 2; mMDHP, mIDH, sAAT, EST, PEPA, ADA, sACOH, and GPI), the green and the blue lizards are completely distinctive from each other, not sharing a single allele. This absence of shared alleles at these eight loci applies to all 21 lizards analyzed from the Paraguana Peninsula. In addition, the lack of shared alleles at these eight loci applies to the 14 lizards analyzed (three blue and 11 green) from the areas of sympatry. Clearly, the green and the blue lizards represent separate lineages for which there is no evidence of hybridization. They are separate species.

Is One of the Species from the Paraguana Peninsula a Local Population of *C. lemniscatus*?

A number of genetic studies have revealed intraspecific geographic variation in allele frequencies within *Cnemidophorus*, even to the extent of apparent fixation of alternative alleles in different populations for one or a very few loci (Cole et al., 1988; Dessauer and Cole, 1989, 1991). Consequently, we do not take the view that two or more populations must share the same alleles at all 39 loci tested in order to be considered conspecific (table 2). For example, consider the locus ESTD. Cole and Dessauer (1993) concluded that the seven specimens they examined from San Ignacio de Yuruani, Venezuela, are *C. lemniscatus*, despite having apparent fixation of the b allele. The a allele of ESTD is apparently fixed in Christiaankondre, Suriname (10 specimens examined), but the a and b alleles both occur in certain populations (e.g., Boa Vista, Brazil). The specimens from San Ignacio de Yuruani and Christiaankondre showed no other fixed genetic differences and they are sufficiently similar morphologically, ecologically, and behaviorally to be regarded as one species.

In this context, we review the genetic data in table 2, comparing the various new population samples with the *C. lemniscatus* from San Ignacio de Yuruani, Venezuela, and all other samples of *C. lemniscatus* discussed by Cole and Dessauer (1993). The green lizards from the Paraguana Peninsula show apparently fixed differences from the *C. lemniscatus* of San Ignacio de Yuruani at eight loci. The lizards from Guyana show apparently fixed differences from the *C. lemniscatus* of San Ignacio de Yuruani at only one locus, ESTD, for which the Guyanan specimens from Yupukari have the a allele typical of specimens from Christiaankondre, the restricted type locality (Cole and Dessauer, 1993). This, together with their morphology, confirms that the lizards from Guyana are *C. lemniscatus*. The blue lizards from the Paraguana Peninsula show apparently fixed differences from those of San Ignacio de Yuruani at only two loci (mIDH and ESTD), but they have the ESTD a allele typical of *C. lemniscatus* from Christiaankondre, and thus differ from them at only mIDH. Clearly, the genetic data indicate that the green lizards from the Paraguana Peninsula are not conspecific with *C. lemniscatus*, but the blue lizards are essentially identical to *C. lemniscatus*, despite their distinctive coloration.

Is One of the Species from the Paraguana Peninsula a Local Population of *C. gramivagus*?

Although no biochemical analyses have been conducted on known specimens of *C.*

←

[m] Frequency = 0.31 to 0.40.

[n] Frequency = 0.41 to 0.50.

[o] Frequency = 0.06 for each of the c, e, and f alleles.

[p] A faster allele (frequency about 0.50; Cole and Dessauer, 1993) occurs at GPI also in this population. A cross-correlation gel was not run to see if it is the same a allele reported here for LEMG. This applies also for ALB, although Cole and Dessauer (1993) did not publish their ALB data; no plasma was available for the Brazilian samples included in that paper.

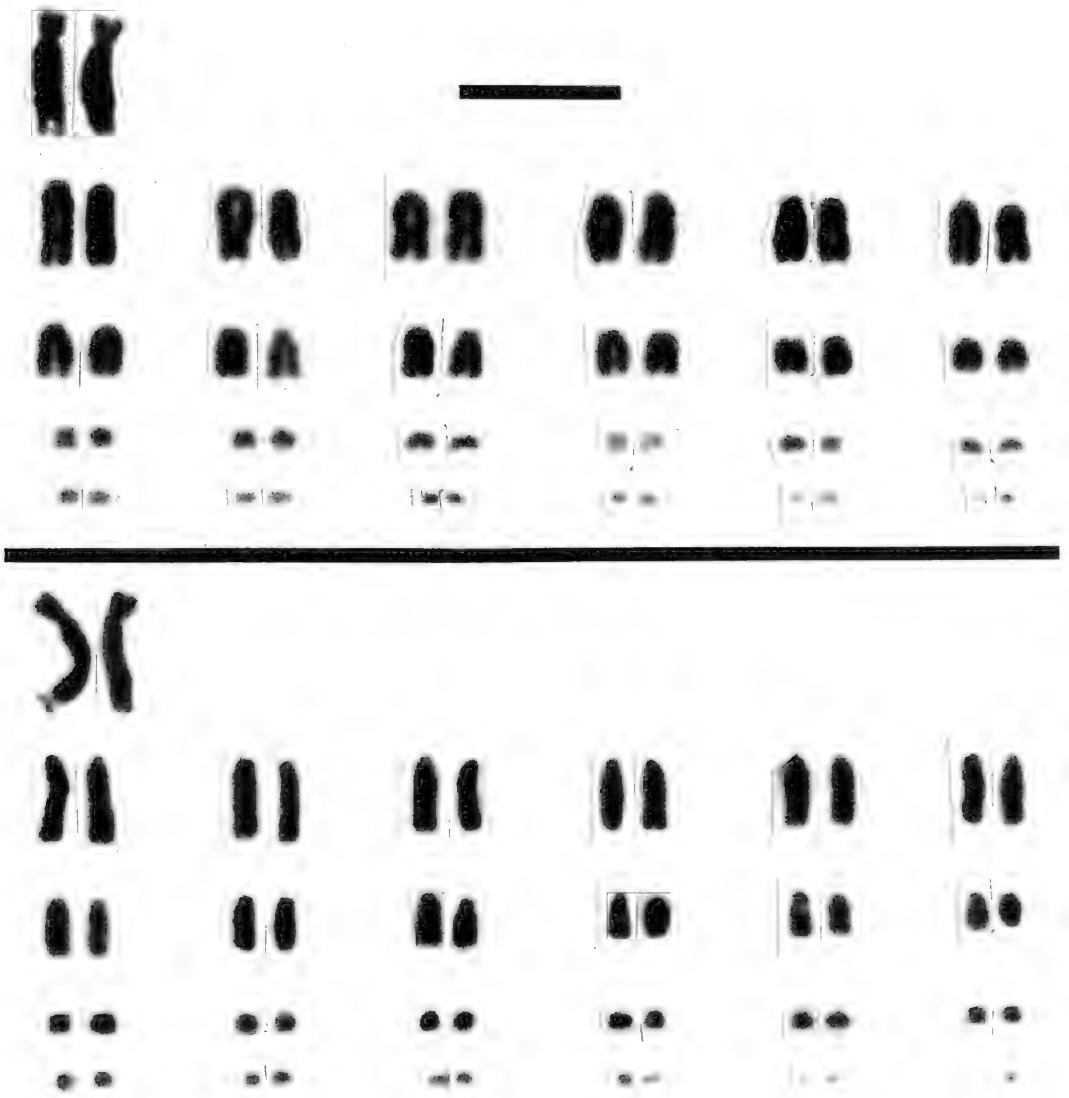

Fig. 2. Diploid karyotypes (2n = 50 chromosomes) of two species in the *Cnemidophorus lemniscatus* complex, each with one pair of large, submetacentric to subtelocentric chromosomes (with a dotlike terminal satellite on the long arm), 12 pairs of microchromosomes, and 12 pairs of telocentric chromosomes of intermediate size. Both lizards are from the Paraguana Peninsula, Venezuela. **Upper**. The green form named below as *C. arenivagus* (AMNH 142585, female). Bar = 10 μm. **Lower**. The blue form named below as *C. l. splendidus* (AMNH 142594, female).

gramivagus, it is appropriate to comment on this question here. Morphologically, the blue lizards from the Paraguana Peninsula show the same distinguishing characters from *C. gramivagus* as do other samples of *C. lemniscatus*, but with the nasal suture passing through the center of the nostril (as in *gramivagus*) at a higher frequency. Morphologically, the green lizards from the Paraguana Peninsula also lack the suite of characters diagnostic of *C. gramivagus*, although they are similar in position of the nasal suture. Consequently, neither species of *Cnemidophorus* on the Paraguana Peninsula represents *C. gramivagus*. As the green and the blue *Cnemidophorus* from the Peninsula are distinctive, they merit distinctive names and descriptions (see below).

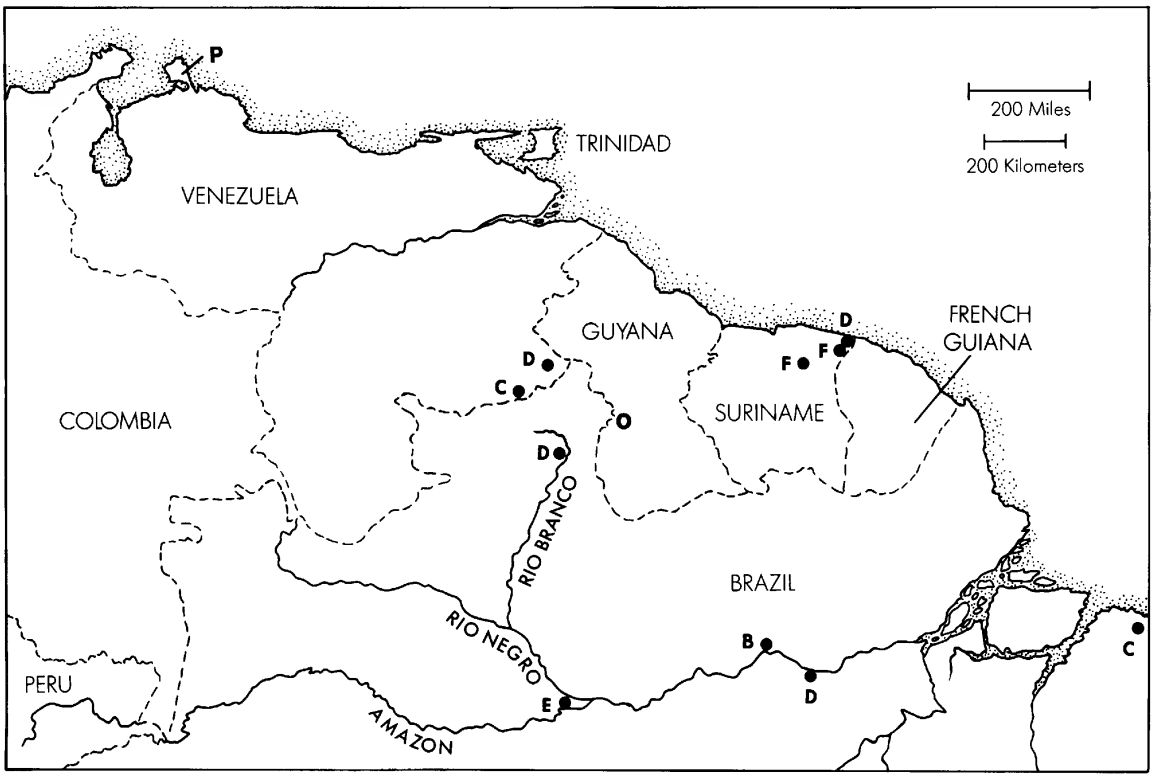

Fig. 3. Map of the Guianan Region of South America showing localities for samples of the *Cnemidophorus lemniscatus* complex compared karyotypically and electrophoretically in the present paper, by Cole and Dessauer (1993), and by Sites et al. (1990). Reproduced and slightly modified from Cole and Dessauer (1993: 12), as follows: O in Guyana represents the site for *C. l. lemniscatus* from Yupukari (table 2, LEMG); and P in northwestern Venezuela represents sample sites for the blue and the green lizards from the Paraguana Peninsula. B and C represent *Cnemidophorus cryptus*, D represents *C. l. lemniscatus*, E represents probably *C. gramivagus*, and F represents *C. pseudolemniscatus*.

Is One of the Species from the Paraguana Peninsula the Second Ancestor of the Unisexual *C. cryptus*?

Cnemidophorus cryptus is a diploid unisexual species of hybrid origin, with the type locality in Venezuela (Cole and Dessauer, 1993). In the absence of genetic data from *C. gramivagus*, but with evidence of one complete haploid genome shared with *C. lemniscatus*, the ancestry of *C. cryptus* was hypothesized to be *C. lemniscatus* × *C. gramivagus*, as no other geographically relevant congeneric bisexual species was known at that time. We now compare the genotype of the new species of green lizards from the Paraguana Peninsula with the non-*lemniscatus* genotype of *C. cryptus* (table 2).

At mMDHP the non-*lemniscatus* allele in *C. cryptus* is b, whereas the green lizards are fixed for a. At mIDH the non-*lemniscatus* allele in *cryptus* is b, whereas the green lizards are fixed for d. At ADA the non-*lemniscatus* allele in *cryptus* is a, whereas the green lizards are fixed for b. At sACOH the non-*lemniscatus* allele in *cryptus* is b, whereas the green lizards are fixed for a. At GPI the non-*lemniscatus* allele in *cryptus* is b, whereas the green lizards are fixed for a. Thus, the green species from the Paraguana Peninsula differs from the second ancestor of *C. cryptus* at five loci. We conclude that the green lizards do not represent the second ancestor of *C. cryptus*. Nevertheless, the green lizards do share with the second ancestor of *cryptus* the same distinctive alleles at three informative loci (table 2; sAAT, PEPA, and PEPB), as well as many other alleles, indicating that they may be close relatives. The hypothesis that

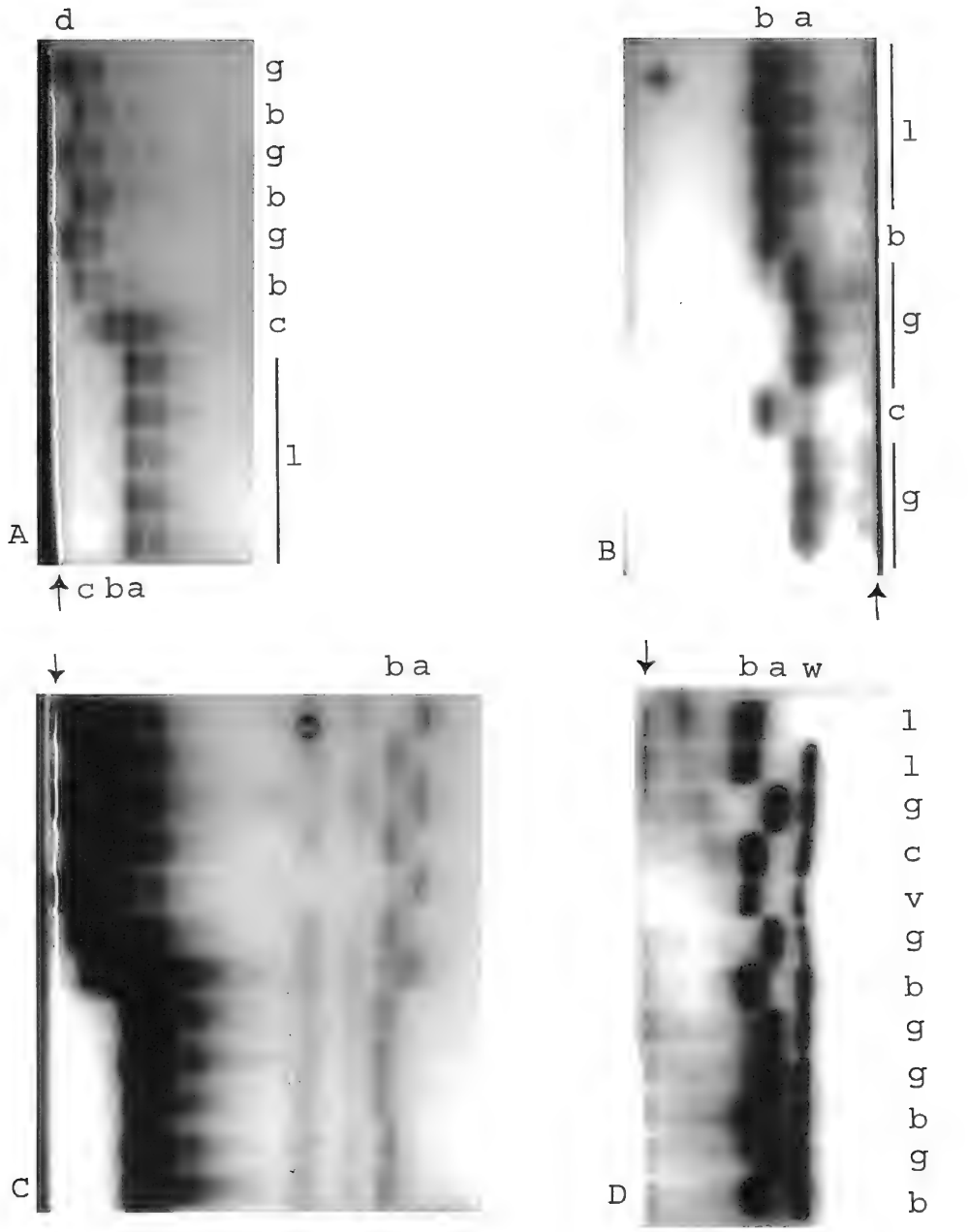

Fig. 4. Electrophoretic patterns of five enzymes on four gels, each including 12 lizards of three or four species of the *Cnemidophorus lemniscatus* complex. **A**. mIDH. **B**. GPI. **C**. PEPA (with alleles designated) developed over MPI and mIDH (same gel as in **A** but developed further). **D**. sMDHP (with w above) and mMDHP (with a and b above). Letters below or above each gel refer to the different allele products (compare with table 2; w, meaning "wild type," is applied to loci showing no allelic variation in this study [table 2, footnote c]). Letters at the right side of three gels identify the lizards, as follows: b, blue lizards from the Paraguana Peninsula named below as *C. l. splendidus*; c, *C. cryptus* from Icabaru, Venezuela; g, green lizards from the Paraguana Peninsula named below as *C. arenivagus*; l, *C. l. lemniscatus* from Yupukari, Guyana; and v, *C. l. lemniscatus* from San Ignacio de Yuruani, Venezuela. A vertical bar beside a letter indicates several individuals of the same group side-by-side. For **C**, arrangement of individuals is identical to **A** (same gel, same orientation). For each gel, anode is to the right, and arrow indicates position of sample applications.

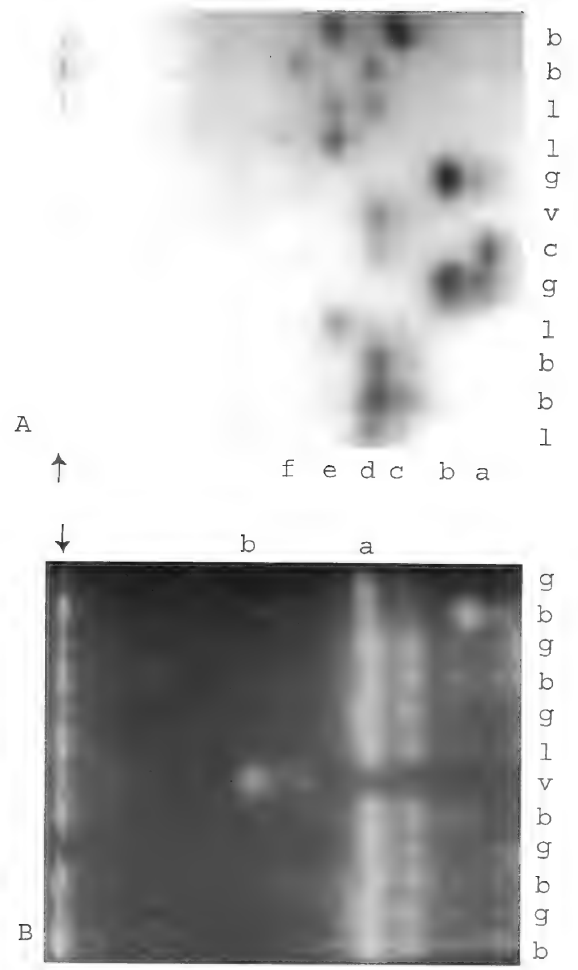

Fig. 5. Electrophoretic patterns of two enzymes on two gels including 12 lizards representing three or four species of the *Cnemidophorus lemniscatus* complex. **A**. ADA. **B**, ESTD. Letters above or below the gels refer to the different allele products (compare with table 2). Letters at the right side of each gel identify the lizards, as in figure 4. Anode is to the right, and arrow indicates position of sample applications.

C. gramivagus is the second ancestor of *C. cryptus* still merits testing.

Evidence from Morphology: Comparisons Among the Blue and the Green Lizards and *C. lemniscatus* from the Guianas

We now analyze external morphology and color pattern to examine the hypothesis suggested by the evidence from biochemical genetics: the green *Cnemidophorus* from the Paraguana Peninsula are conspecific neither with the sympatric blue lizards nor with *C. lemniscatus* of the Guianan Region, and the latter two are much more closely related to each other than either is to the green species.

Sexual Dimorphism

Sexual dimorphism of color pattern and size has been commonly reported within the genus *Cnemidophorus* (e.g., McCrystal and Dixon, 1987; Cole and Dessauer, 1993), but little information exists about dimorphism of scalation. We found sexual dimorphism in all three groups of lizards (blue, green, and *lemniscatus*) in several characters (tables 3, 4), two of size (the proportion of head length to snout-vent length, and total length) and two of scalation (number of gular scales, and number of scales around midbody). Males are normally larger than females, and the higher number of scales around midbody of males may be related to this size difference. Dimorphism of the gular scales also may be related to size differences as most males have a noticeably larger and wider head than do females, as reflected by the HL/SVL ratios. Male head size is often larger than that of females in macroteiids (Vitt et al., 1993).

The green lizards are interesting with respect to sexual dimorphism, as they were found to be uniquely dimorphic in three additional characters: number of finger lamellae, number of femoral pores, and shape of the posterior margin of the central enlarged preanal shield.

Univariate Comparisons

Affinities among means or character state distributions were calculated for 17 characters of size, shape, and scalation (tables 4, 5), to examine similarities and differences among the three groups of lizards. Two characters (number of interlabial scales, number of scales between medial femoral pores) exhibited no differences among any of the groups, and three characters (number of finger lamellae, number of toe lamellae, and position of nostril with respect to the nasal suture) differed significantly among all three groups. Position of the nostril was more similar in blue lizards and *lemniscatus* than either was to that in green lizards (fig. 6). The same pattern of blue lizard and *lemniscatus*

TABLE 3

Descriptive Statistics and Sexual Dimorphism of Characters in *Cnemidophorus* from the Paraguana Peninsula and the Guianan Region

Character[a]	Sex[b]	Group[c,d]	N	Mean (±SE)	Range	SD
COS		B	37	11.6 (±0.2)	8–14	1.5
		G	71	11.5 (±0.2)	8–16	1.6
		L	53	12.6 (±0.2)	9–15	1.3
GUL	Male	B**	27	24.6 (±0.4)	21–29	1.9
		G**	37	20.7 (±0.2)	18–23	1.2
		L**	32	23.6 (±0.3)	19–27	1.9
	Female	B	8	22.3 (±0.4)	21–24	1.2
		G	30	20.1 (±0.2)	18–21	1.0
		L	17	21.7 (±0.4)	20–25	1.6
ILS		B	38	7.8 (±0.3)	4–14	2.0
		G	73	7.4 (±0.3)	2–13	2.6
		L	55	7.2 (±0.3)	2–12	2.2
FP	Male	B	28	46.2 (±0.6)	41–53	3.1
		G**	39	42.1 (±0.4)	36–49	2.6
		L	34	45.4 (±0.3)	39–52	3.2
	Female	B	8	44.9 (±0.9)	39–47	2.6
		G	32	40.2 (±0.4)	35–47	2.5
		L	21	44.1 (±0.7)	39–52	3.4
IFS		B	38	2.4 (±0.1)	1–4	0.7
		G	72	2.7 (±0.07)	1–4	0.6
		L	55	2.6 (±0.08)	2–4	0.6
FLS	Male	B	27	30.9 (±0.4)	26–36	2.0
		G*	40	35.0 (±0.2)	31–37	1.5
		L	30	32.9 (±0.5)	29–40	2.6
	Female	B	9	30.3 (±1.0)	25–34	3.0
		G	31	34.3 (±0.2)	31–37	1.3
		L	21	31.6 (±0.5)	27–36	2.3
TLS		B	36	56.8 (±0.6)	51–66	3.5
		G	71	66.0 (±0.4)	57–74	3.4
		L	50	60.5 (±0.6)	54–75	4.0
SAB	Male	B*	26	105.8 (±1.3)	95–118	6.6
		G*	38	94.5 (±0.8)	84–105	5.1
		L***	34	113.0 (±1.3)	99–131	7.4
	Female	B	8	98.6 (±3.0)	85–110	8.4
		G	29	91.0 (±0.9)	81–101	5.1
		L	20	104.8 (±1.3)	96–115	5.9
SPV		B	35	12.1 (±0.4)	8–19	2.7
		G	74	11.4 (±0.2)	9–17	1.7
		L	55	19.5 (±0.4)	15–28	2.9
SPV/SAB		B	32	.118 (±0.004)	.072–.171	0.025
		G	65	.123 (±0.002)	.090–.168	0.016
		L	54	.178 (±0.003)	.130–.230	0.021
SVL (in mm)	Male	B	29	71.2 (±1.4)	50–80	7.5
		G*	40	68.4 (±1.6)	34–85	10.1
		L*	34	65.3 (±2.1)	39–87	12.1
	Female	B	9	61.2 (±0.9)	58–65	2.6
		G	33	61.8 (±1.3)	40–77	7.7
		L	21	56.8 (±1.7)	43–69	8.0

TABLE 3—(*Continued*)

Character[a]	Sex[b]	Group[c,d]	N	Mean (±SE)	Range	SD
TOTL (in mm)	Male	B**	19	250.1 (±6.5)	185–289	28.5
		G***	26	248.7 (±5.5)	183–300	28.2
		L*	16	207.6 (±10.5)	132–282	42.0
	Female	B	5	209.4 (±5.1)	200–225	11.3
		G	19	208.8 (±5.9)	146–257	25.8
		L	7	170.6 (±9.2)	159–183	9.2
SVL/TOTL[e]		B	22	.265 (±0.003)	.265–.319	0.014
		G	34	.287 (±0.002)	.262–.311	0.013
		L	11	.308 (±0.004)	.294–.349	0.015
HL/SVL[e]	Male	B***	20	.297 (±0.003)	.277–.322	0.011
		G***	34	.267 (±0.002)	.249–.290	0.010
		L***	21	.290 (±0.002)	.270–.307	0.009
	Female	B	7	.255 (±0.002)	.255–.273	0.006
		G	19	.247 (±0.005)	.231–.321	0.020
		L	10	.269 (±0.003)	.258–.283	0.009

[a] See Methods for meaning of abbreviations.

[b] Characters exhibiting a significant ($P < .05$) degree of sexual dimorphism are presented with separate statistics for each sex.

[c] Group designations: B = blue animals from Paraguana; G = green animals from Paraguana; L = *Cnemidophorus lemniscatus* from eastern Venezuela, Guyana, and Suriname.

[d] Asterisks (*) indicate significant *P*-levels derived from *t*-tests for sexual dimorphism; * < .05; ** < .01; *** < .001. See table 4 for tests between populations.

[e] Specimens > 60 mm SVL were used.

similarities and their differing in green lizards was observed in five more characters of scalation (shape of anal spur in males, number of femoral pores, number of gulars, shape of the posterior margin of the central enlarged preanal shield [fig. 7], and number of scales around midbody). Also, adult green animals generally had a relatively shorter head than adults of the other two groups (figs. 8 and 9). Parallel slopes within sexes in log head length (HL) versus log snout-vent length (SVL) were observed in the three groups ($P < .90$ in males, $< .30$ in females), and in an ANCOVA both log HL and the covariate, log SVL, were highly significant ($P < .001$). With body size corrected for, a Bonferroni test revealed a similar head size in male blue lizards and male *C. lemniscatus*, both of which differed from the green males ($P < .001$ in each case). The head size of female green lizards, however, was similar in female blue lizards ($P < .12$) and differed from *C. lemniscatus* ($P < .01$); the blue females and *C. lemniscatus* females were similar to each other ($P < .75$).

Frontonasal shape (fig. 10) was roughly hexagonal or octagonal in the blue lizards and *C. lemniscatus*, but basically rhomboidal in green animals.

Total length was smaller in *C. lemniscatus* than in the other two, but this may have been influenced by sampling bias. However, the ratio of snout-vent length to total length showed the same pattern and suggests that *Cnemidophorus lemniscatus* has a shorter tail than the blue and the green lizards of the Paraguana Peninsula.

Thus, the group affinities indicated by the morphological characters generally support the hypothesis suggested by the biochemical data. The green lizards are most distinctive and the blue lizards are most similar to *C. lemniscatus*.

Multivariate Analysis

Results of two principal components analyses (PCAs), using 13 characters (males) and 12 characters (females, excluding ASPUR), are shown in table 6 and figures 11 and 12. Principal components (PC) I and II combined represented about 50% of the variance in

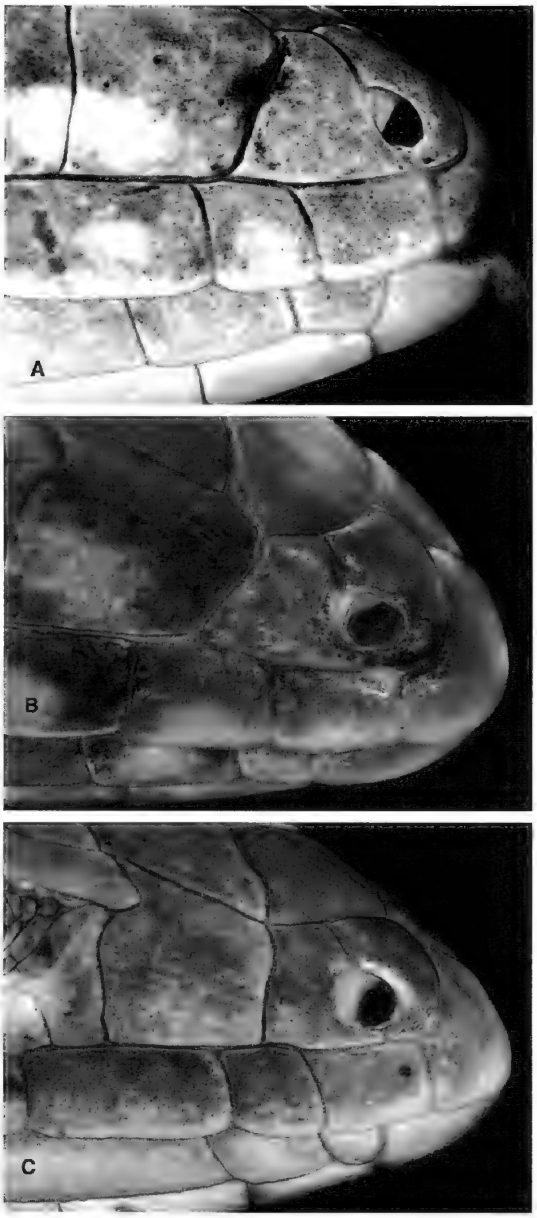

Fig. 6. Position of nostril in relation to nasal suture. **A**. Nostril is far anterior to suture and suture almost borders nostril posteriorly (character state 1); *Cnemidophorus l. lemniscatus*, AMNH 133299, from Suriname. **B**. Suture is more anterior (state 2); blue lizard (named *Cnemidophorus l. splendidus* below), AMNH 142589, Paraguana Peninsula. **C**. Nostril is approximately centered in suture (state 3); green lizard also from the Paraguana Peninsula (named *C. arenivagus* below), AMNH 142582.

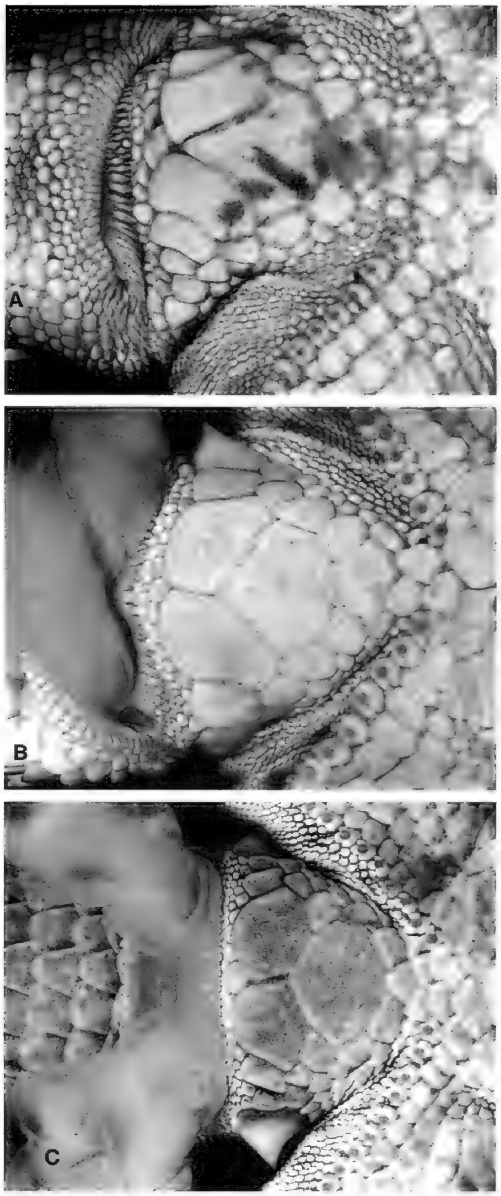

Fig. 7. Three character states of the enlarged central preanal shield (CPAS) in *Cnemidophorus* from the Paraguana Peninsula. **A** and **B**. Acute and nearly acute angles, respectively, on the posterior edge, as in green lizards (named *C. arenivagus* below); AMNH 142586 and AMNH 142583, respectively. **C**. Obtuse angle on the posterior edge, as in blue lizards (named *Cnemidophorus l. splendidus* below); AMNH 142589. For *Cnemidophorus l. lemniscatus* from the Guianan Region, CPAS is similar to that in **C**.

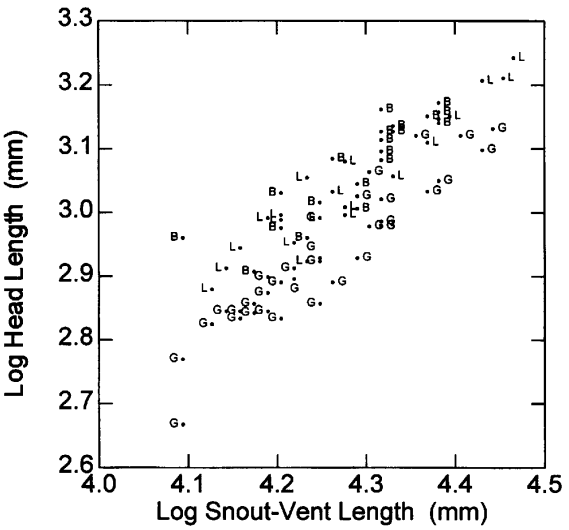

Fig. 8. Scatterplot of log head length as a function of log snout-vent length in adult males (≥ 60 mm SVL) of the *Cnemidophorus lemniscatus* complex. Letters indicate taxa, as follows: B, blue lizards from the Paraguana Peninsula (named *Cnemidophorus l. splendidus* below); G, green lizards from the Paraguana Peninsula (named *C. arenivagus* below); and L, *Cnemidophorus l. lemniscatus* from the Guianan Region.

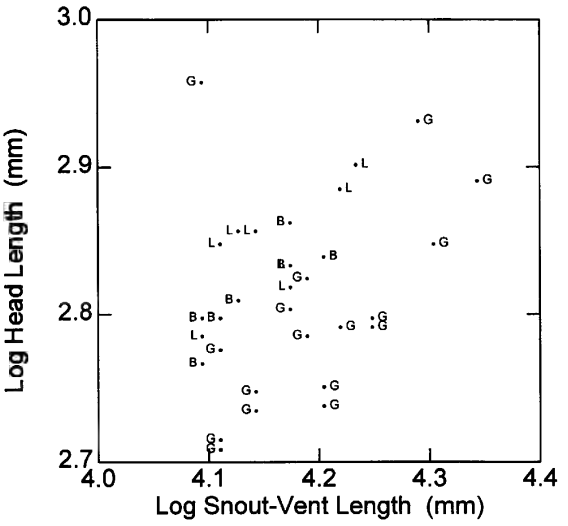

Fig. 9. Scatterplot of log head length as a function of log snout-vent length in adult females (≥ 60 mm SVL) of the *Cnemidophorus lemniscatus* complex. Letters as in figure 8.

both male and female analyses and PC III and IV about 20% more. The latter two had eigenvalues slightly greater than 1.00 but did not reveal new information about character importance or intergroup relationships.

Variable loadings were similar along PC I of males and females (r_{10} = .9351; P < .001, without ASPUR), and this axis completely separates the green lizards from both the blue animals and *C. lemniscatus*, although the latter two broadly overlap each other. Position of the nostril with respect to the nasal suture, shape of the posterior margin of the central enlarged preanal shield, scales around midbody, number of gulars, granules between paravertebral stripes, and shape of the anal spur in males all contribute significantly to PC I and may reflect character concordance, as found in a PCA of several members of the *Cnemidophorus neomexicanus* complex by Cole et al.(1988).

PC II reflected variation associated with differences between the blue lizards (B) and *C. lemniscatus* (L), and loadings of variables were also correlated between the male and female analyses, although somewhat weaker than on PC I (r_{10} = .7582; P < .01; table 6). The variance associated with PC II was less than half that of PC I, indicating fewer differences between the blue animals and *lemniscatus* than between both of these groups and the green lizards. B and L clusters are visually and statistically distinct (figs. 11 and 12); male B and male L scores on PC II, despite showing some overlap (fig. 11), are very different (t_{42} = -4.825; P < .001). High loadings on PC II of the males are due to the numbers of finger and toe lamellae, circumorbital scales, scales between medial femoral pores, and granules between the paravertebral stripes; those on PC II of the females are due to number of scales between the medial femoral pores, interlabial scales, and granules between the paravertebral stripes.

Principal components analyses again produce the same results obtained by both the biochemical genetic data and univariate analyses of morphology. The green lizards are most distinctive among all of these animals, and the blue lizards are most similar to *C. lemniscatus*.

Variation in Color Pattern

"Any general description must disregard the maze of lesser details of variation which, when hundreds of individuals are examined,

TABLE 4

Affinities of Continuous Character Means Between Groups of the *Cnemidophorus* Examined

Character[a]	Sex[b]	Affinity[c]
COS		B———G *** L ** B
GUL	Male	B *** G *** L———B
	Female	B ** G ** L———B
ILS		B———G———L———B
FP	Male	B *** G *** L———B
	Female	B *** G *** L———B
IFS		B———G———L———B
FLS		B *** G *** L ** B
TLS		B *** G *** L *** B
SAB	Male	B *** G *** L *** B
	Female	B * G *** L———B
SPV		B———G *** L *** B
SPV/SAB		B———G *** L *** B
SVL (in mm)	Male	B———G———L * B
	Female	B———G * L———B
TOTL (in mm)	Male	B———G ** L ** B
	Female	B———G ** L ** B
SVL/TOTL		B———G *** L *** B
HL/SVL	Male	B *** G *** L———B
	Female	B *** G *** L———B

[a] See Methods for meaning of abbreviations.

[b] Data given separately by sex if character is sexually dimorphic in at least one group.

[c] Group designation as in table 3. A solid line indicates no significant intergroup difference at $P < .05$. Asterisks (*) indicate significant P-levels derived from Tukey HSD or Mann-Whitney tests: * ≤ .05; ** ≤ .01; *** ≤ .001.

TABLE 5

Meristic Characters and Their Affinities Between Groups of the *Cnemidophorus* Examined

Character/ State[a]		Groups B	Groups G	Groups L	Affinity[b,c]
NAS	1	0	0	35	B *** G *** L *** B
	2	34	1	20	
	3	4	68	0	
ASPUR	1	0	12	17	B *** G *** L———B
	2	28	13	0	
	3	5	6	35	
CPAS[d]	1	0/0	8/20	0/0	Males:
	2	0/0	17/12	0/0	B *** G *** L———B
	3	0/0	8/1	2/1	
	4	3/1	7/0	3/0	Females:
	5	26/8	1/0	22/15	B *** G *** L———B
	6	0/0	0/0	7/5	

[a] See Methods for abbreviations and character states.

[b] Group designations as in table 3.

[c] Associated P-levels derived from the Mann-Whitney U-statistic and designated as in table 3.

[d] A slash (/) indicates values for males/females.

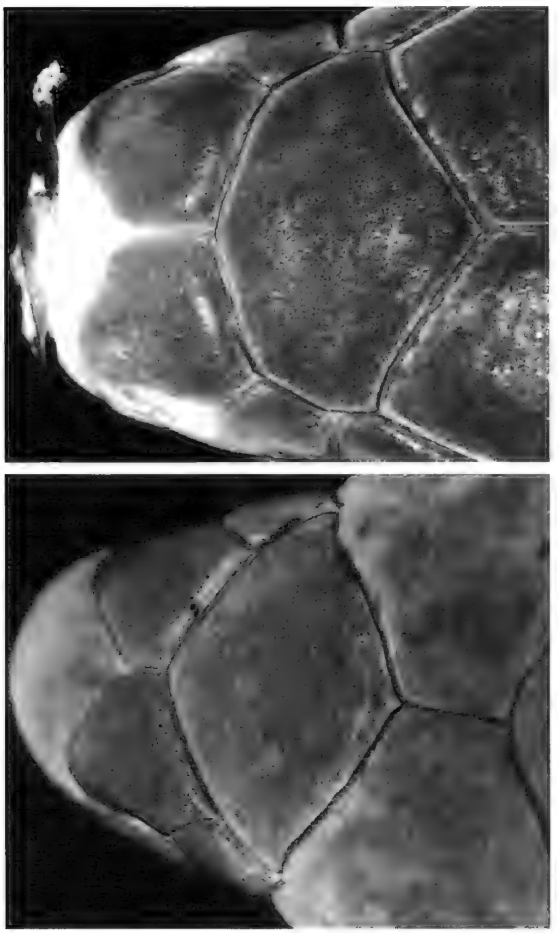

Fig. 10. Frontonasal scales of different shapes in *Cnemidophorus* from the Paraguana Peninsula. **Upper**. A blue lizard (named *Cnemidophorus l. splendidus* below); AMNH 142592. **Lower**. A green lizard (named *C. arenivagus* below); AMNH 142582. The frontonasal of *Cnemidophorus l. lemniscatus* from the Guianan Region is similar to that in the upper lizard.

would require chapters of endless minutiae," said William Beebe (1945: 17) of color patterns of *Cnemidophorus lemniscatus* he observed in Kartabo, Guyana and in Carapito, Venezuela. We found a similar labyrinth of ontogenetic, sexual, and geographic variation of color pattern in the three groups we studied. Also, color changes in preservative often misrepresent coloration in life. Here we consider the ontogenetic, sexual, and intergroup components of color pattern variation in the blue and the green lizards and compare them with *C. lemniscatus*.

Juveniles have a dark brown or black

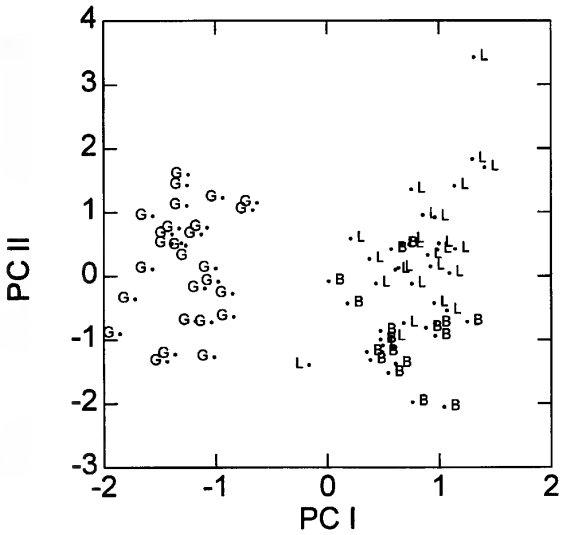

Fig. 11. Scores on the first two principal components (PC) extracted from the correlation matrix of 13 morphological characters of males of the blue (B) and the green (G) *Cnemidophorus* from the Paraguana Peninsula and of *Cnemidophorus l. lemniscatus* (L) from the Guianan Region. Additional information on the PCA is presented in table 6.

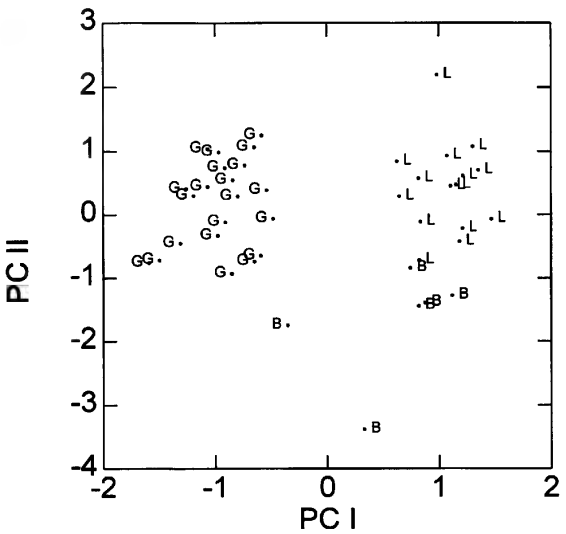

Fig. 12. Scores on the first two principal components (PC) extracted from the correlation matrix of 12 morphological characters of females of the blue (B) and the green (G) *Cnemidophorus* from the Paraguana Peninsula and of *Cnemidophorus l. lemniscatus* (L) from the Guianan Region. Additional information on the PCA is presented in table 6.

TABLE 6
Principal Components of Scalation and Size in Male and Female *Cnemidophorus* Examined

	Principal component loadings			
	Males[a]		Females[b]	
Variables	I	II	I	II
ASPUR	0.780	0.101	—	—
COS	0.169	0.510	0.163	0.298
FLS	−0.423	0.810	−0.635	0.145
FP	0.565	0.201	0.551	−0.229
GULAR	0.745	0.016	0.652	−0.343
IFS	−0.102	0.506	0.118	0.721
ILS	0.091	−0.034	−0.299	−0.450
NAS	−0.894	0.023	−0.937	0.014
CPAS	0.867	0.047	0.931	−0.116
SAB	0.826	0.327	0.783	0.072
SVL	0.134	0.058	−0.558	−0.268
SPV	0.655	0.497	0.752	0.389
TLS	−0.559	0.640	−0.697	0.292

[a] Male sample: (n) = B(17), G(27), L(27); eigenvalues, (I) = 4.700, (II) = 1.994; percentage of variance, (I) = 36.2, (II) = 15.3.

[b] Female sample: (n) = B(6), G(21), L(15); eigenvalues, (I) = 4.981, (II) = 1.329; percentage of variance, (I) = 41.5, (II) = 11.1.

ground color, which usually changes with growth to light brown, green, or blue (figs. 13 and 14) in adults. However, adult female lizards of the blue type often have a black or very dark brown ground color (figs. 15 and 16). An ontogenetic reduction in number of light stripes at midbody occurs in males of all three groups but not in females (table 7; fig. 15); number of stripes and snout-vent length were negatively correlated in males (Pearson correlational test, $P < .001$ in all groups) but not in females. Juvenile males usually have 8, 9, or 10 light stripes and adults from 3 to 6. This change occurs primarily with loss of the third and second lateral stripe, in that order (figs. 17 and 18). Occasionally these stripes are represented by a collinear series of spots that may be interconnected (or not) by thin, faint lines in adults.

Sexual dimorphism of adult color pattern is expressed in differences in stripe number (table 7) and often but not always in ground color (fig. 16). Females of the blue type usually are not blue; they usually have light yellowish tan or gold stripes on a dark brown or black ground color, whereas the males are a brilliant, striking metallic royal blue (figs. 13C and 14C). However, two females (MCNG 1167 and AMNH 142590) collected near Miraca at a locality of sympatry with the green lizards were blue like the males. In the Aguaque area, several but not all males of the blue type displayed broad, bright orange or orangish tan lateral patches and a few females had reduced orange patches in the ventrolateral trunk area also. These lateral patches may vary in intensity with the seasons, as apparently they do in males of *C. lemniscatus* in the Guianan Region.

Most adult males of the green type from the Paraguana Peninsula display a bright green or yellow-green ground color (fig. 13A), occasionally with bright yellow or orange to tan lateral patches, but three males over 70 mm snout-vent length (SVL) in our sample were brown. The largest females (> 67 mm SVL) of the green type were invariably green like the males, but adults of 58–67 mm SVL could be either green or brown. Two adult green females kept in captivity for three years displayed seasonal shifts in the brilliance and intensity of their coloration. Both were predominantly green but periodically they attained particularly vivid and brilliant hues in almost all aspects of their dorsal, lateral, and cephalic coloration.

Males of *C. lemniscatus* are like males of the green taxon in that the largest specimens display a greenish ground color (figs. 13 and 14). The largest females of *lemniscatus*, however, are brown rather than green like the largest females of the green taxon.

Some large blue males and green males and females displayed a blue or green hue in the middorsal area, which often obfuscated the middorsal pattern of stripes (fig. 14C). This may be a color change related to breeding condition, as suggested by Schall (1973) for the specimens on Aruba Island that he referred to *Cnemidophorus lemniscatus* (but we refer these to the new green taxon, below). The greenish hue appeared more frequently in populations of green lizards south of Adicora in November-December, 1990, during the typical short wet season of the Peninsula, than in June and July in other years. However, some blue and some green lizards with such hues were observed in most

populations at any time of the year. One of the two green females mentioned above displayed periodic color brilliance in captivity, acquiring this green hue, but the hue disappeared after a few months and the dorsal stripes again became readily recognized.

The dorsal hue may be related to age as well as reproductive state. A large blue male kept in captivity for three years initially had bold dorsal light stripes of yellowish tan color but gradually acquired a permanent, slight greenish wash in the light dorsal stripes, which became less distinct but nevertheless recognizable. Also, the brilliance of its general blue ground color faded and then brightened again later, much as in the captive green females mentioned above. The dorsal striping pattern is often obscure in both the largest blue and largest green individuals.

Several features of color pattern differed consistently between the green lizards, the blue lizards, and the *C. lemniscatus* we examined. The *lemniscatus* exhibited a split vertebral stripe (table 8; also see discussion below, Taxonomic and Evolutionary Considerations) and a much higher number of granules between the paravertebral stripes (table 3) than did the blue or the green lizards. Blue animals are similar to green ones in these two characters but differ in possessing their brilliant blue color. Also, juveniles and adult females of the blue form tend to have a darker ground color, often nearly black in appearance, than in the green form (fig. 16).

Some green animals had one or two elongate, ovoid tannish cream spots on the posterior thigh, which gives the appearance of a regular or irregular stripe. In contrast, *C. lemniscatus* and blue animals have a series of three to five spots that are rarely interconnected and normally appear separate on the posterior thigh. However, this character varies widely in green lizards, so its taxonomic utility is questionable.

The number of light stripes at midbody and condition of the second and third lateral stripes also showed intergroup differences in adult males (table 7; figs. 17 and 18). Blue lizards had a lower modal number of stripes, usually around three, than green lizards and *C. lemniscatus*, both of which had five. The first lateral stripe of blue lizards was often discontinuous and represented by a series of collinear dots.

Two other color pattern characters were difficult to quantify and impossible to record from preserved specimens. The presence of small ventrolateral turquoise spots in females were observed in the blue form and *C. lemniscatus* but not in green lizards. These spots are often most numerous behind the arm rather than more posteriorly and often extend ventrally to the edge of the first row of ventral scales.

The color of the dark paravertebral and dark dorsolateral stripes is noteworthy also. These areas are very dark brown to black in the blue form and *C. lemniscatus* but medium brown to light brown in the green animals. Also, the paravertebral dark brown stripes of the green lizards are often only lightly suffused with a blackish pigment, contributing to the generally lighter appearance of green animals.

The nature of the vertebral striping may also be related to the generally lighter appearance of the green lizards (figs. 13 and 14). The vertebral light stripe is often sharply defined in *C. lemniscatus* and blue animals, contrasting well with the dark background, and is usually only a few granules wide. However, the vertebral light stripe is almost always somewhat diffuse or subtle in green lizards.

Coloration of the blue and the green *Cnemidophorus* of the Paraguana Peninsula probably evolved as adaptations to different habitats, as discussed below.

ECOLOGY

The Paraguana Peninsula of northwestern Venezuela has a surficial area of 2570 km^2 and is continuous with the mainland by a long narrow isthmus, the Istmo de Medanos (figs. 3, 23 and 24). Its climate is arid (Koeppen classification Aw″(s″)i) with an annual rainfall of from 284 mm (Las Piedras on the west coast) to 453 mm (Coro, just south of the Peninsula) occurring primarily in a brief wet season from mid-October to mid-December (Walter and Medina, 1971; Sarmiento, 1976). Almost continuous east/northeast winds have generated duneland formations on the southeastern peninsular coast, the isth-

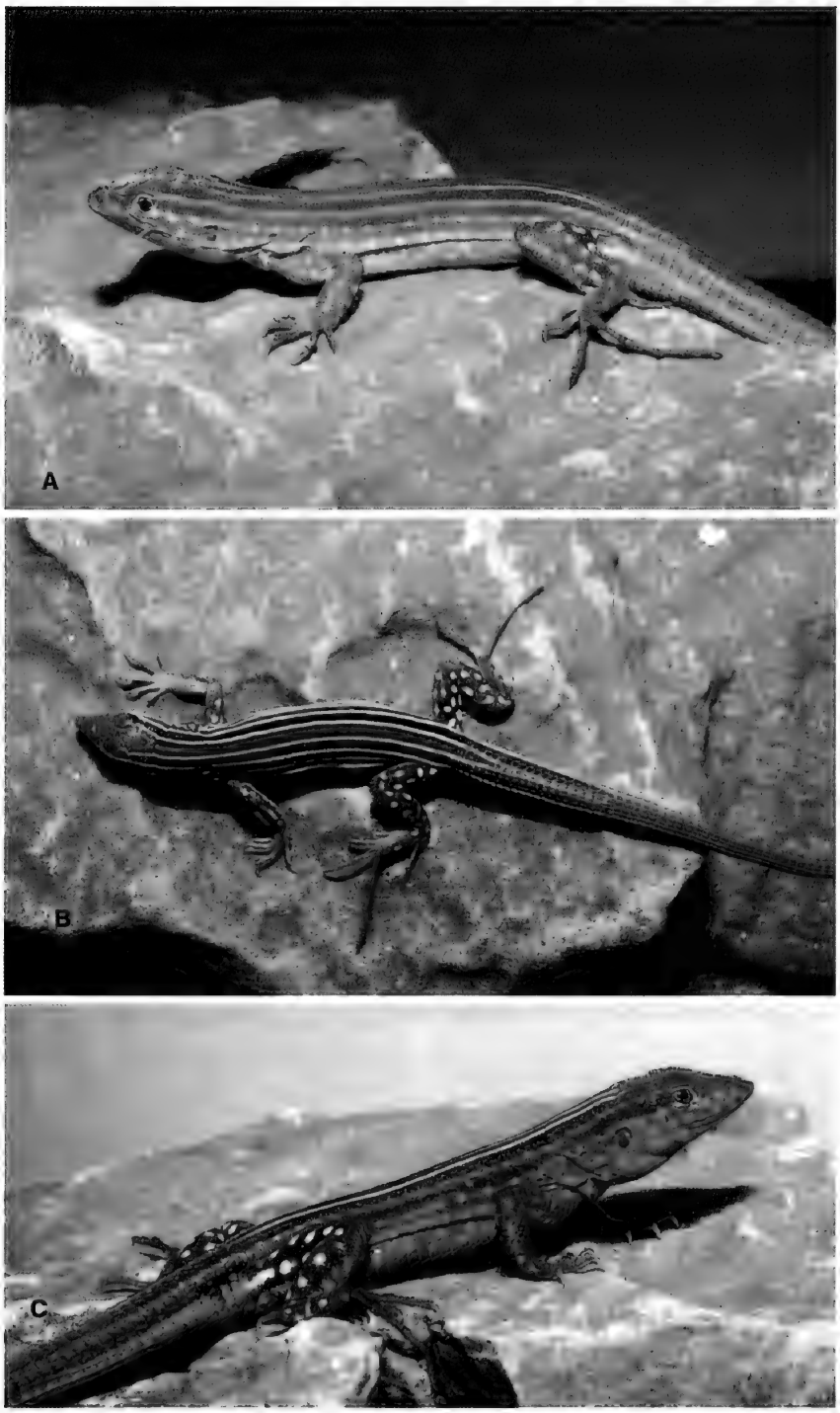

Fig. 13. Two species of *Cnemidophorus* from the Paraguana Peninsula, Venezuela. **A** and **B**. Adult male and juvenile, respectively, of the green lizard (named *C. arenivagus* below); holotype, MCNG 1402, snout-vent length 71 mm, and juvenile male, paratype, AMNH 142587, snout-vent length 53 mm, respectively. **C**. Adult male of the blue lizard (named *C. l. splendidus* below); holotype, MCNG 1403, snout-vent length 80 mm.

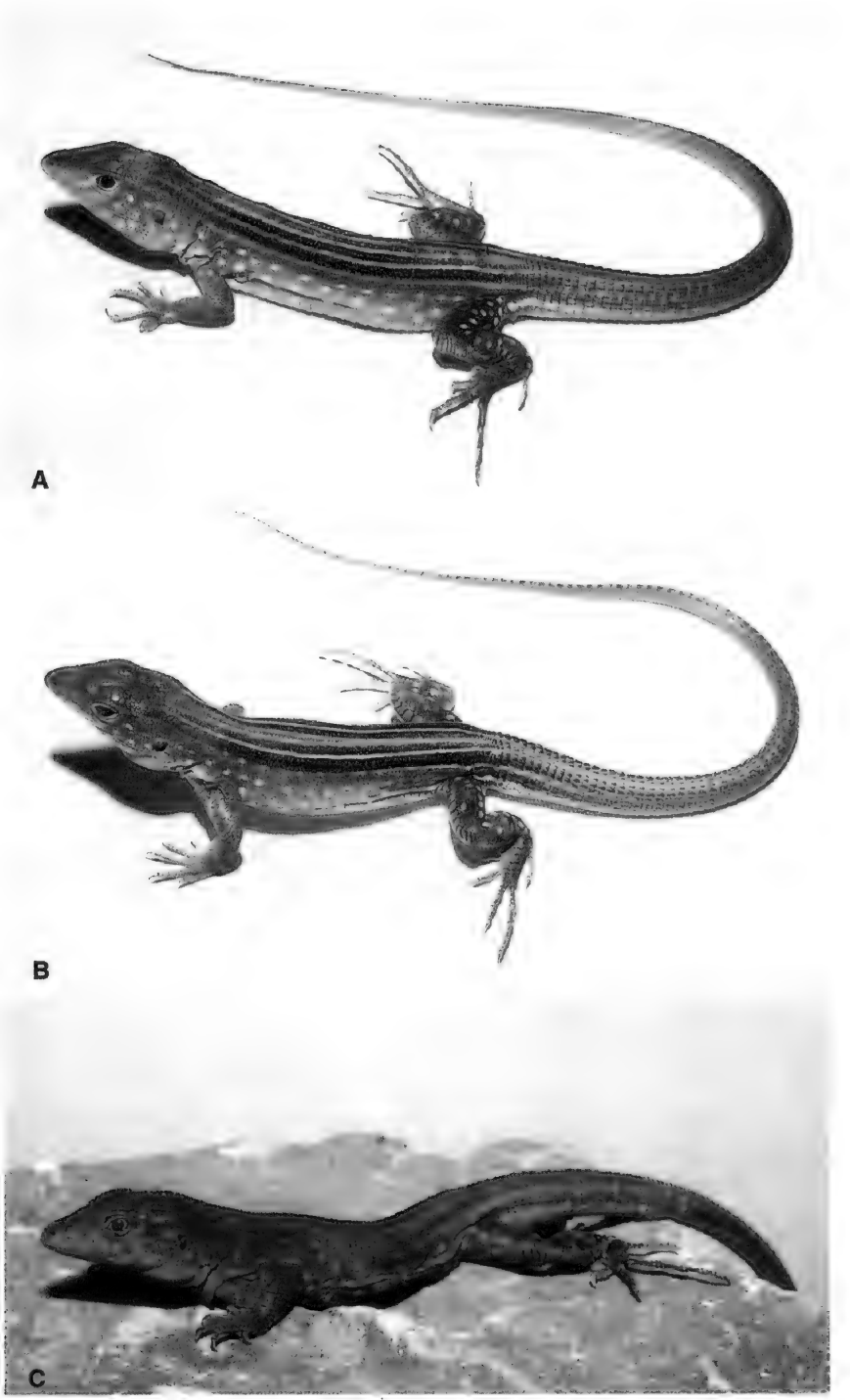

Fig. 14. Three specimens of *Cnemidophorus lemniscatus* from northern South America. **A** and **B**. *C. l. lemniscatus* from Suriname (AMNH 133295, snout-vent length 86 mm) and, respectively, from Guyana (AMNH 138079, snout-vent length 71 mm). **C**. Adult male of the blue lizard from the Paraguana Peninsula (named *Cnemidophorus l. splendidus* below; paratype, AMNH 142595, snout-vent length 73 mm).

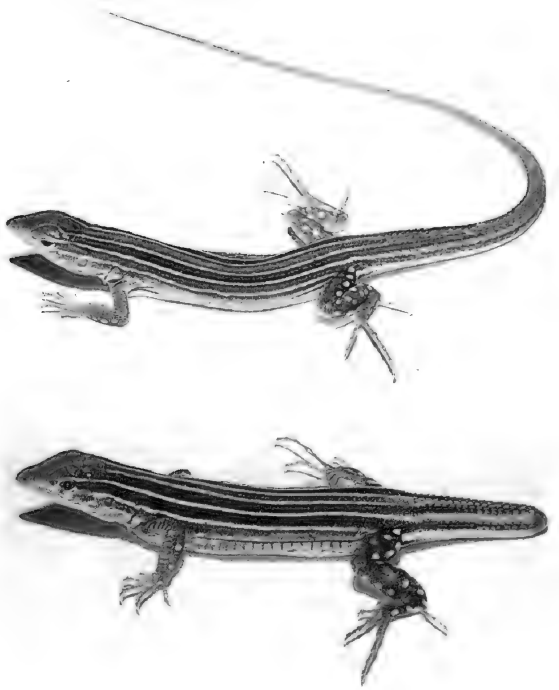

Fig. 15. Adult females of *Cnemidophorus* from the Paraguana Peninsula. **Upper**. The green lizard (named *C. arenivagus* below); paratype, AMNH 142588, snout-vent length 68 mm. **Lower**. The blue lizard (named *C. l. splendidus* below); paratype, AMNH 142594, snout-vent length 62 mm.

mus, and adjacent mainland areas. Much of the Peninsula is a flat lowland punctuated by several areas of significant elevation, such as Cerro Santa Ana (850 m; figs. 19, 20) and Fila de Monte Cano (240 m; fig. 19), in the southeastern portion; these areas are part of a ridge, the Buena Vista highlands.

Dominant plant communities on the Peninsula are similar to those of other northwestern Venezuelan arid areas and include duneland, desert and desert scrub, thorn woodland, and the less common dry evergreen bushland (Sarmiento, 1976; Rivero-Blanco and Dixon, 1979). Santa Ana and Monte Cano are ecologically more complex and have additional plant communities owing to local topography and microclimates (Bevilacqua et al., 1988; Markezich and Taphorn, 1994). Agricultural activities of the medium/high density human population (10–25/km^2) has adversely affected much of the natural vegetation of the Peninsula, and many areas of thorn woodland and dry evergreen bushland have been destroyed. Apparently more forest existed only several hundred years ago, since Spanish records from the early 16th century allude to high abundance of deer and other animals associated with forest communities (Gaspirini et al., 1985), and relicts of indigenous settlements occur in what are presently desertified, inhospitable areas particularly around the Santa Ana area.

A study of whiptail distribution in 1990 along an east-west road that begins off the coastal road 10 km south of Adicora and continues west over a salt flat to Miraca clearly demonstrated that the blue and the green *Cnemidophorus* are associated with distinctly different habitats (fig. 19). Only green animals were in the desert and desert scrub communities on the east side of the salt flat. Just west of the salt flat, desert and desert scrub grades rather sharply into thorn woodland, and the two species were sympatric here; green animals were observed in the low scrub areas and on the open, desertic roadsides, while blue lizards occurred next to these in the thorn woodland. Further down the road, at 8 km west of the coast, only thorn woodland occurred; only blue animals were observed here and from this point on to Miraca. The microgeographical distributions of the blue and the green lizards in the southeastern section of the Peninsula reflect these different ecological distributions (fig. 19).

The open habitats of the green *Cnemidophorus* include dunes (fig. 20), beaches, desert, and desert scrub (referred to as "thorn scrub" by Sarmiento, 1976), all communities of very low physiognomy (seldom 2 m, often 1 m or less) and sparse ground cover (often only 2–3%). In dunelands on the coast, small patches of vegetation exist irregularly in large, bare areas of sand and contain various grasses of the genus *Sporobolus* and short plants and shrubs such as *Lycium* (Solanaceae), *Castela* (Simarubaceae), *Heliotropium*, and vinelike *Tournefortia* (Boraginaceae) (Tamayo, 1941). Occasionally the mesquite tree, *Prosopis juliflora* (Mimosoideae), a common element of the peninsula, grows

TABLE 7
Distribution of Number of Light Stripes at Midbody in Various Color Pattern, Sex, and Size Groups of the *Cnemidophorus* Examined

Group[a]	Number of stripes[b]											Mean
	0	1	2	3	4	5	6	7	8	9	10	
BM, Adults		1	3	10	8	5						3.5
Juv.									1	1		8.5
BF, Adults				1	1		1		2	2		6.7
Juv.									1	1		8.5
GM, Adults	1		1		10	7	9	1	4	2		5.4
Juv.										6		6.0
GF, Adults						1	2	2	11	6		7.9
Juv.								1	5	5		7.8
LM, Adults						10	6	2			3	6.2
Juv.								1		10	1	8.9
LF, Adult						1			1	6	2	8.7
Juv.										10	1	8.3

[a] First letter of designated color group is same as in table 1. Second letter designates male (M) or female (F). Adults are ≥ 60 mm SVL; juveniles are < 60 mm SVL.

[b] A blank space indicates no observation in that category; otherwise, number of lizards observed is presented.

in these associations on the leeward side of dunes, particularly on the Isthmus. Desert and desert scrub communities just west of the dunes are flat and include these floral elements as well as abundant cacti (*Opuntia*) in some areas. Small patches of grasses are common and very few tall trees such as *Prosopis* occur in this association. Where vegetation patches in relatively open ground occurred in these associations, lizards were often observed around the patches or traveling from patch to patch, which presumably provided sites for foraging and thermoregulation.

The common habitat of the blue *Cnemidophorus* on the Paraguana Peninsula is thorn woodland (Sarmiento, 1976), often called "mattoral" (fig. 21). The canopy of this xeric community is open, the vegetation profile higher (often 2–4 m), and percentage ground cover greater (10–75%) than in the open habitats. *Prosopis juliflora* is usually quite common along with other trees and shrubs such as *Castela*, *Jacquinia* (Theophrastaceae), *Croton* (Euphorbiaceae), various mimosoids, and the cacti *Opuntia* and *Mammilaria*. In some areas, the tall columnar cactus *Stenocereus griseus* is quite conspicuous, often reaching heights of 6 m. Many of the other plants and grasses associated with the open desert and desert scrub communities are found in the understory of the thorn woodland, and abundant annual herbaceous ground cover is evident during the short wet season. The amount of shade is greater than in the open habitats occupied by the green lizards, due to the taller and often denser vegetation.

Blue lizards are also associated with the edges of and occasionally within the dry evergreen bushland community (Sarmiento, 1976), also referred to as "very dry tropical forest" by others (Rivero-Blanco and Dixon, 1979). The dominance of sharp-spined *Bromelia humilis* (Bromeliaceae) as ground cover often precludes access to this community by large lizards, but blue animals were occasionally observed to take shelter under the bromeliads when pursued. This community is much rarer than thorn woodland on the peninsula, and much of it has apparently been destroyed as elsewhere in the Caribbean arid areas (Rivero-Blanco and Dixon, 1979). Limited patches of it exist in Monte Cano, Santa Ana, and other areas in the Buena Vista highlands.

Relictual patches of dry forest (often called "tropical deciduous forest"; see Sarmiento, 1976) occur in the Monte Cano area (see Markezich and Taphorn, 1994), but blue animals have not been observed directly in

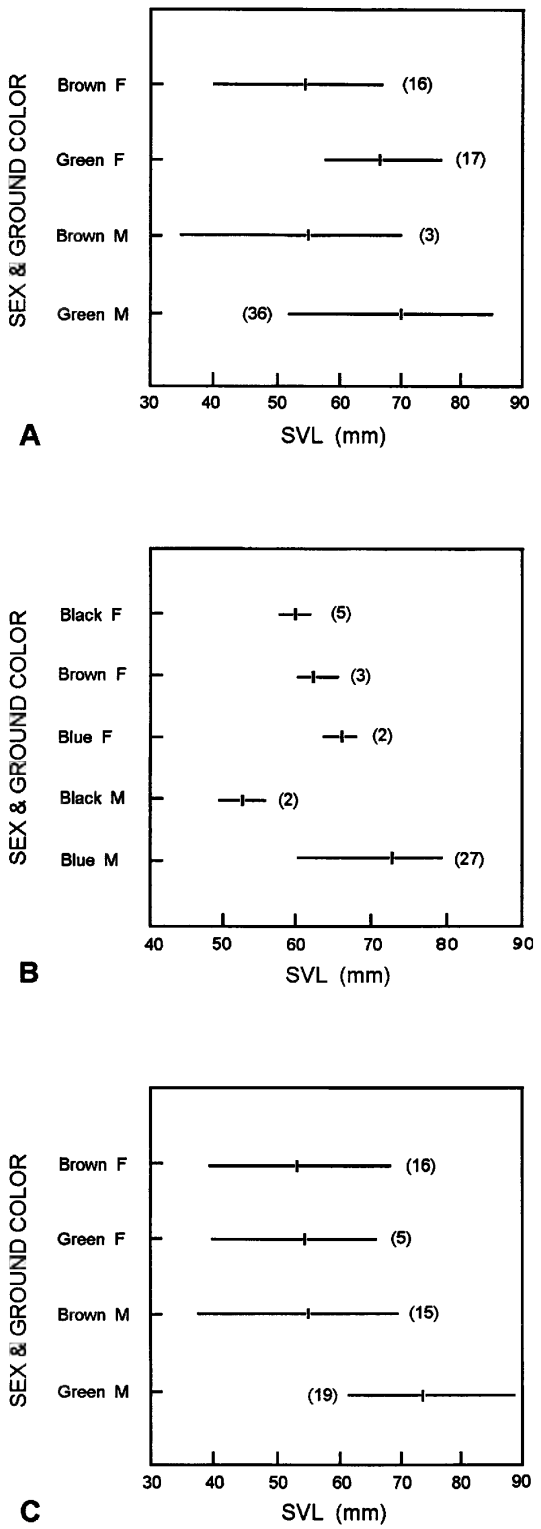

Fig. 16. Relationship between ground color in life and sex and size in three taxa of *Cnemidophorus*. **A**. The green lizards (named *C. arenivagus* below) from the Paraguana Peninsula. **B**. The blue lizards (named *Cnemidophorus l. splendidus* below) from the Paraguana Peninsula. **C**. *Cnemidophorus l. lemniscatus* from Guyana and Suriname. Horizontal line represents size range (with sample size); vertical bar represents the mean; F, females; M, males.

this habitat, possibly because little sunlight penetrates the closed canopy.

While the blue and the green lizards on the Paraguana Peninsula are normally allopatric or narrowly parapatric, areas disturbed by human agricultural activities often have unnatural, sharp habitat gradients, and two areas of sympatry were found in such places. In addition to the area along the road to Miraca mentioned above, sympatry occurred at a goat corral and adjacent overgrazed areas on a ranch south of Miraca (fig. 19). This locality was surrounded by thorn woodland habitat of the blue lizards, and green animals were in the open, disturbed areas. At an artificial water impoundment northwest of Adicora, blue animals were found next to the impoundment where various trees and shrubs grow, while green animals were in the surrounding open areas. No evidence of hybridization was found in our genetic or morphological analyses of specimens from the areas of sympatry.

While we did not quantify microhabitat usage by the blue and the green lizards at the localities of sympatry, our observations indicated that they were allotopic (utilized different microhabitats). The microhabitats can best be described by reference to Pianka's (1986) ten microhabitat categories of terrestrial desert lizards; these are essentially based on occurrences of undisturbed lizards in sun or shade in the open or near different vegetational formations. Both the blue and the green animals were sometimes observed in the open but more commonly near vegetational formations, and the microhabitats associated with sun or shade of grass, bush, and tree formations were partitioned by them. Blue animals utilized high bush and tree sun and shade in areas with dense bush cover (fig. 21), while the green ones were associated with grass and low bush sun and

TABLE 8
Number of Specimens Associated with Vertebral Stripe Character States in Three Color Pattern Groups of the *Cnemidophorus* Examined

Group[a]	Vertebral stripe		
	Split	Single	Absent
B	0	21	17
G	0	31	43
L	50	4	1

[a] Group designations as in table 3.

shade in open areas (fig. 20). This allotopic pattern generally reflected the preferred habitats related to their microgeographic distributions. Habitat is often the most common resource partitioned by sympatric lizards (Toft, 1985).

Magnusson et al. (1986) hypothesized that soil type may be important in the ecological separation of closely related *Cnemidophorus* taxa in northern South America. Within our study area on the Paraguana Peninsula (fig. 19), hardpan aridosols are the most widespread soil, loose soils of restricted duneland areas on the coast are entisols, and inceptosols are restricted to the higher elevations of the Buena Vista highlands (MARNR, 1985). Two observations suggest that the physiognomy and degree of openness of vegetation are much more important factors than soil type in the ecological separation of the blue and the green lizards: (1) the green lizards occur on duneland entisols as well as aridosols of open desert scrub and disturbed areas within the tropical thorn woodland communities; and (2) at localities of sympatry the soil, while not analyzed by us, was classified by MARNR (1985) as a singular type and appeared uniform in the microhabitats of the blue and the green whiptails. Thus, while soil type is a primary determinant of vegetation (Krebs, 1994) it does not in itself appear to be a primary factor in the ecological separation of these two lizards on the Paraguana Peninsula.

The climate and habitats of the blue and the green *Cnemidophorus* of the Paraguana Peninsula differ markedly from the relatively humid savanna habitats of the *C. lemniscatus* we studied from eastern Venezuela, Guyana, and

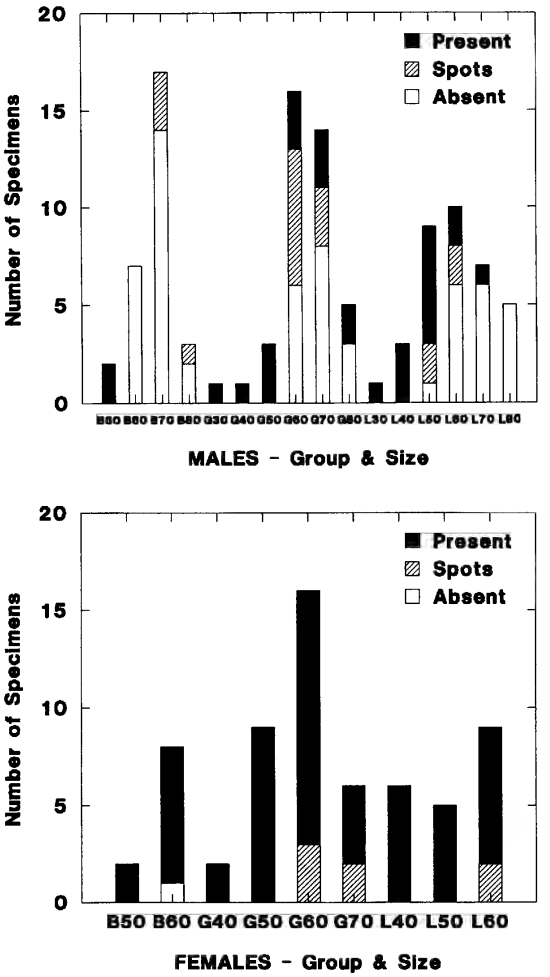

Fig. 17. Relationship between sex, size, and appearance of the second lateral light stripe in three taxa of *Cnemidophorus* from South America. **Upper**. Males. **Lower**. Females. Interpretation: B, the blue lizards (named *Cnemidophorus l. splendidus* below) from the Paraguana Peninsula; G, the green lizards (named *C. arenivagus* below) from the Paraguana Peninsula; L, *Cnemidophorus l. lemniscatus* from the Guianan Region; number following letter on horizontal axis is the smallest snout-vent length in a range of 10 mm size classes; "spots" indicates the stripe is represented by a collinear series of small spots.

Suriname. Observations of *C. lemniscatus* in sandy areas with bushes near beaches in Estado Miranda and Distrito Federal, Venezuela, by one of us (ALM) indicated associations with vegetational profiles and degrees of openness similar to those of the blue lizards on the Paraguana Peninsula, although the species of plants were different. The significance of this

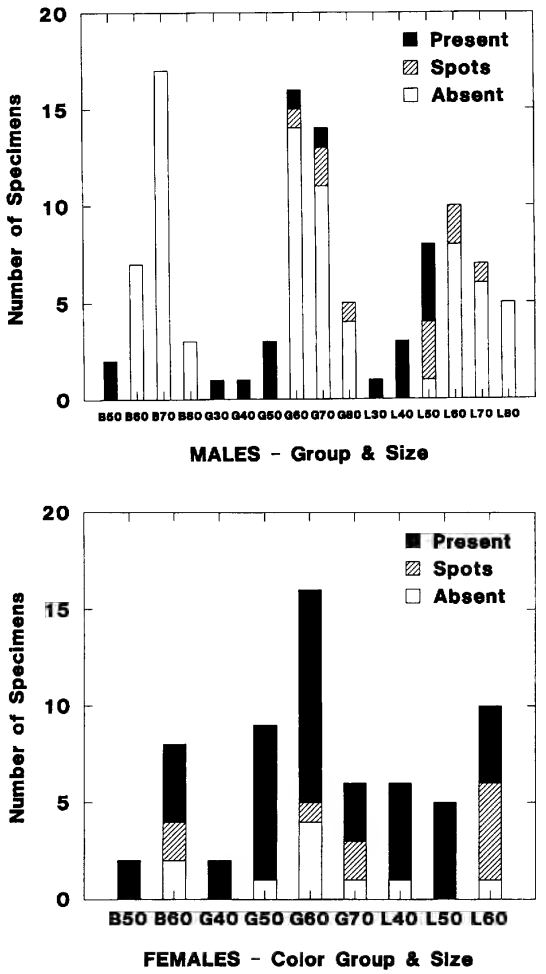

Fig. 18. Relationship between sex, size, and appearance of the third lateral light stripe in three taxa of *Cnemidophorus* from South America. **Upper**. Males. **Lower**. Females. Interpretation as in figure 17.

remains to be demonstrated by future studies, including comparisons with additional samples of lizards from localities spanning these widely separated areas (fig. 3).

Our field observations indicate that the color patterns of the blue and the green lizards serve a protective function (cryptic coloration), although we have not studied possible thermoregulatory or behavioral functions of color pattern, which are commonly found (Norris, 1967; Porter, 1972). Both male and female blue lizards are noticeably darker than the green ones (figs. 13 and 14). Stationary blue lizards were often difficult to see in the meandering shadows of the thorn woodland canopy, and moving animals were often visually lost during collection attempts. Similarly, green animals were difficult to detect when motionless near grass clumps in open areas. The yellow or orange sides apparently enhance crypsis, especially if the lizard is viewed laterally from a distance. Also, they often have light flecks which appear almost glistening in life on the darker dorsal components of their color patterns, perhaps resulting from selection for color matching with a sandy, highly reflective substrate. Background color matching has been demonstrated in other species of lizards (Gibbons and Lillywhite, 1981), particularly *Cnemidophorus inornatus gypsi* of White Sands National Monument, New Mexico (Wright and Lowe, 1993).

Both blue and green lizards were diurnal and active in sunlight from 09:30 to 16:00 hrs on normal, clear days on the Paraguana Peninsula. During the brief annual rainy season in November–December 1990, they were not observed during daily cloudy periods but began basking with the appearance of the sun. Temporal activity patterns appeared to be similar at the localities of sympatry.

The body temperatures of the blue and the green lizards were high and similar to those observed by Schall (1973) in basking *Cnemidophorus* that he referred to *C. lemniscatus* on nearby Aruba Island (probably conspecific with the green animals described here; see Comments in the species description below). The body temperatures were also similar to those of *C. lemniscatus* in northern Brazil (Vitt and de Carvalho, 1995) and *Cnemidophorus deppii* in Nicaragua (Vitt et al., 1993), which thermoregulate behaviorally within a relatively narrow range also, as do other species of *Cnemidophorus* (Bowker, 1993). During July 1993, several air (T_a) and body (T_b) temperatures were recorded in both the blue and the green animals. The T_b of four adult green animals that were basking near grass clumps at 10:00–11:00 hrs in a population 6 km south of Adicora ranged from 36.0 to 37.3°C (mean = 36.6°C) in an air temperature of 32.8°C. Two more green adults both exhibited a T_b of 37.0°C in a T_a of 33.0°C at 12:00 hours at another locality nearby. Body temperatures of blue lizards that were basking near *Prosopis* trees

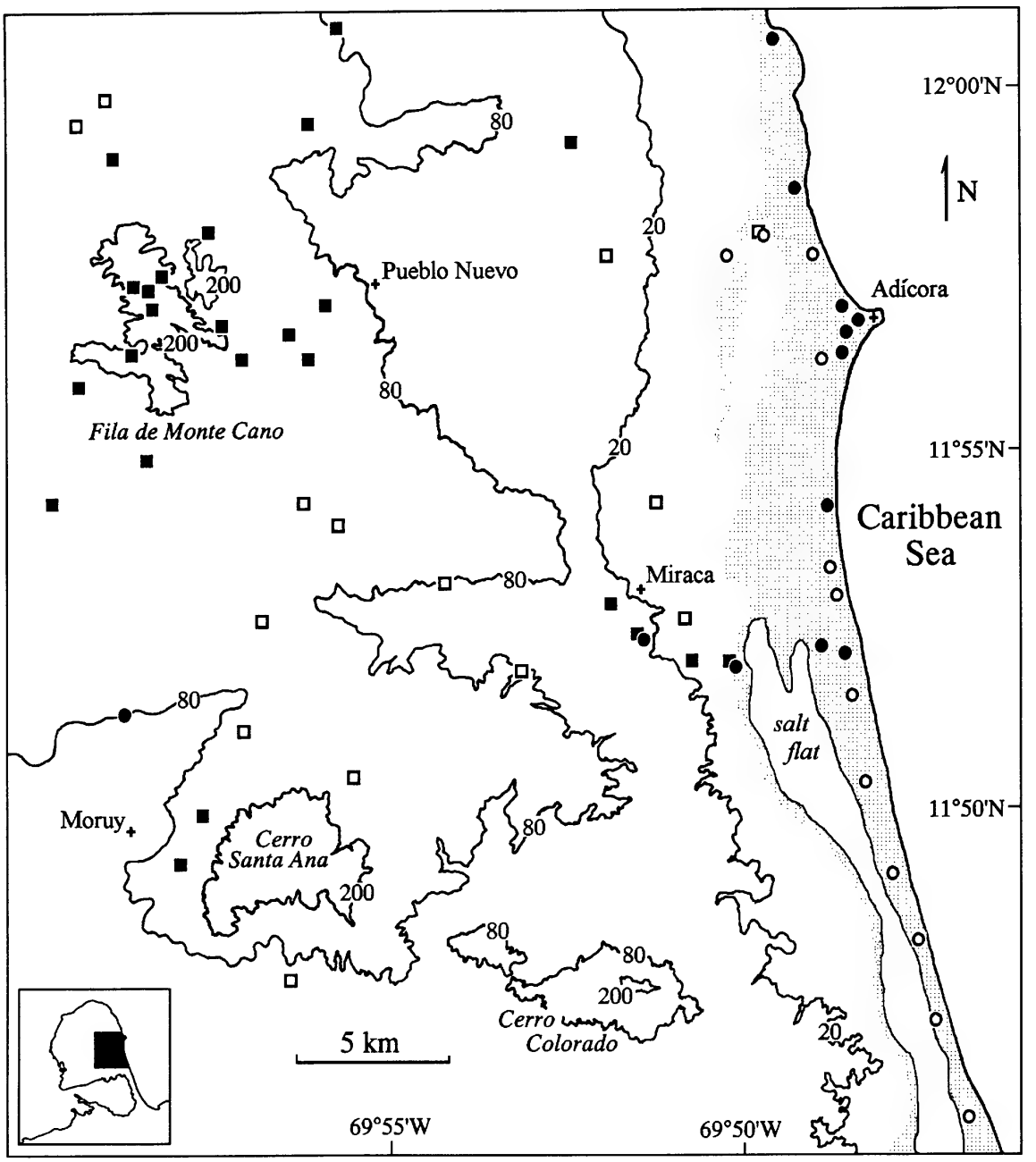

Fig. 19. Microgeographic and ecological distribution of the blue (squares; named *C. l. splendidus* below) and the green (circles; named *C. arenivagus* below) *Cnemidophorus* in the southeastern quadrant of the Paraguana Peninsula. Stippling near the coast indicates duneland or open desert scrub communities; to the west of this is primarily thorn woodland except in the Monte Cano and Santa Ana areas where additional, more complex plant communities occur. Both the blue and the green lizards occur to the west of this area, in appropriate habitats, all the way to the west coast of the Peninsula. Overlap of symbols indicates localities of sympatry. Closed symbols represent specimens collected, open ones specimens observed but not collected. Numbers on contour intervals are elevation (m).

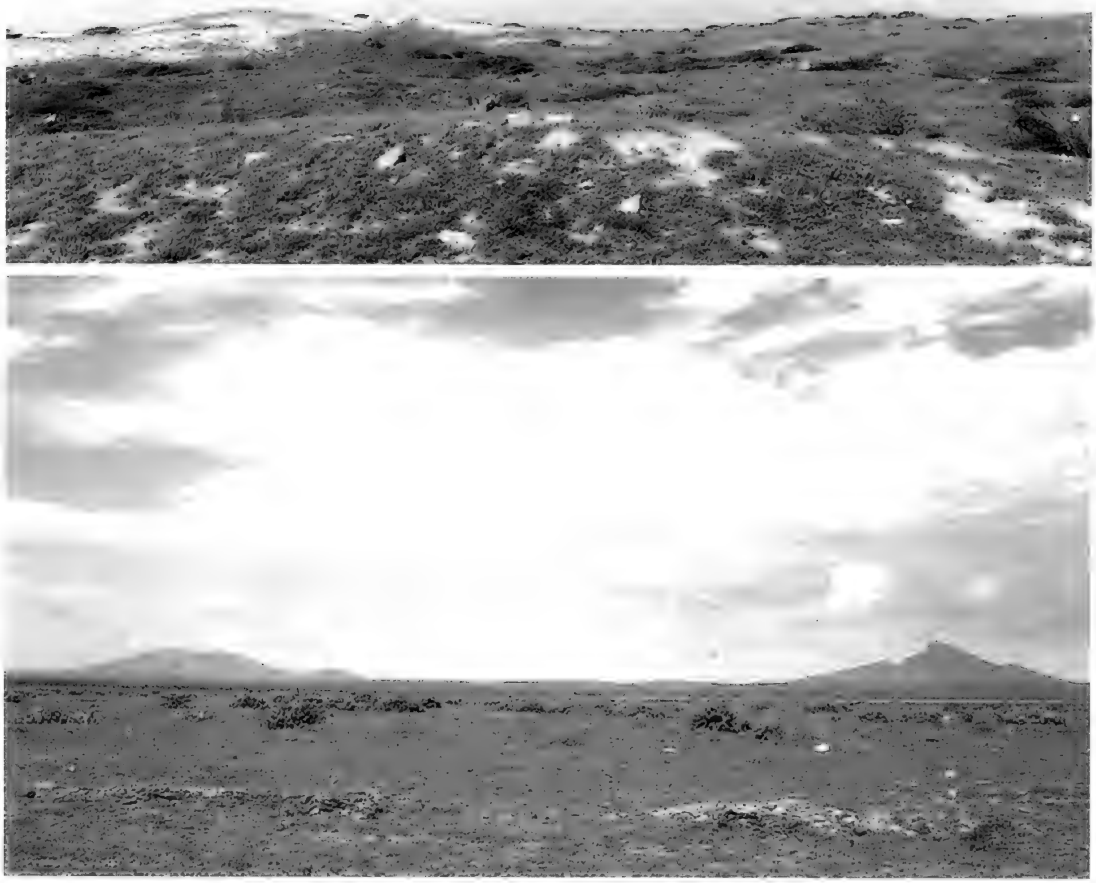

Fig. 20. Habitats of the green whiptail lizard (named *C. arenivagus* below), Estado Falcon, Venezuela. **Upper**. Open sand duneland 20 km north of Coro, Istmo de Medanos. View is to the east; the Caribbean coast is just beyond the hills in the background. **Lower**. Open desert scrubland off the coastal road 10 km south of Adicora, Paraguana Peninsula. View is to the west/southwest, with Cerro Colorado in the left background and Cerro Santa Ana in the right background.

were similar to those of green ones; at Aguaque the afternoon T_b of four blue adults was 35.3–38.9°C (mean = 37.0°C) in T_as ranging from 33.3 to 35.7°C.

Acute color changes, which modify absorbency and reflectance in relation to thermoregulation in many desert lizards (Norris, 1967), were not observed in green or in blue *Cnemidophorus*. However, the green lizards display a very light venter, which probably aids thermoregulation by substrate reflectance, as found in some other desert species (Norris, 1967).

Several physical aspects of the soil burrows

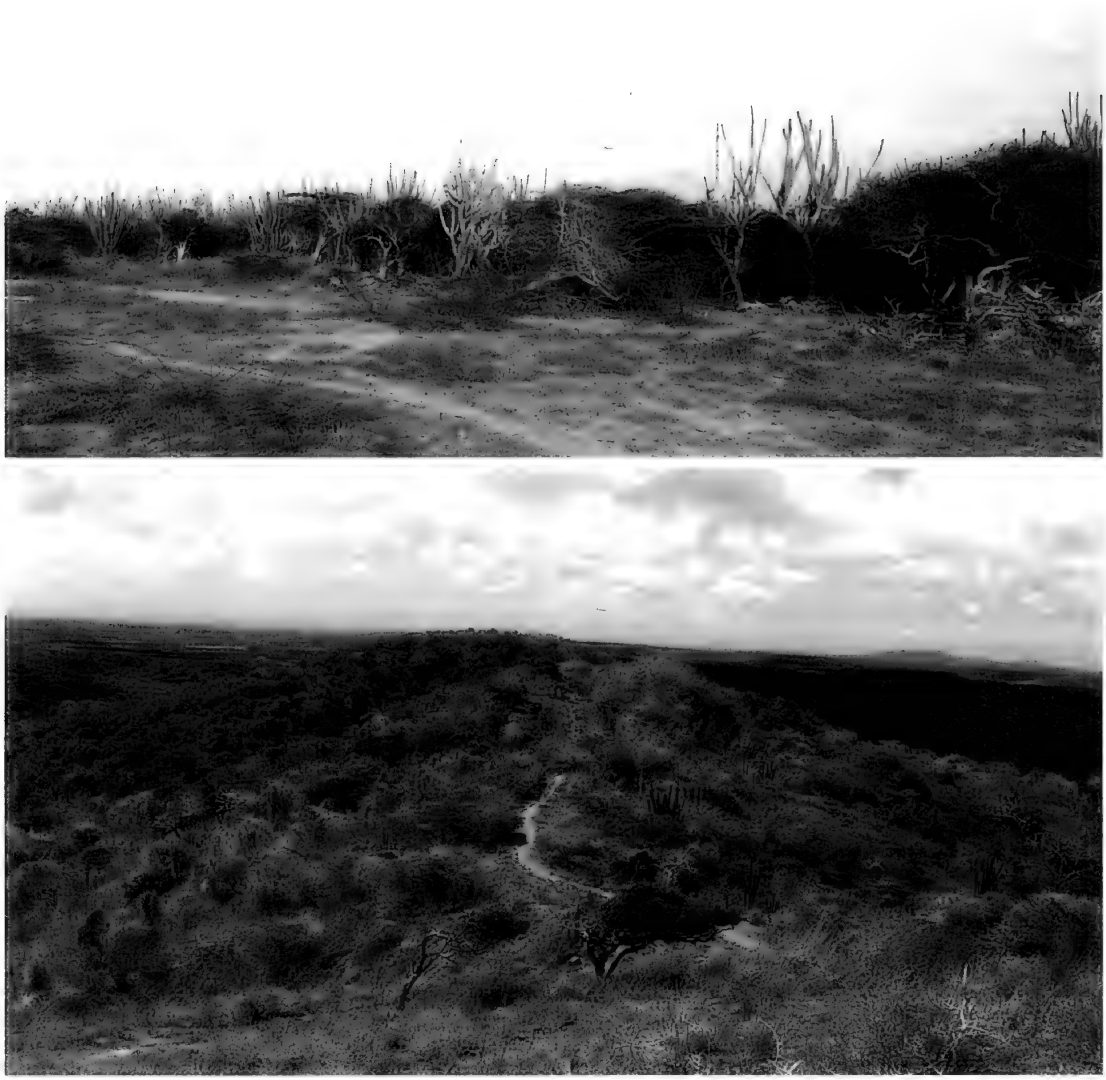

Fig. 21. Habitats of the blue whiptail lizard (named *C. l. splendidus* below) on the Paraguana Peninsula, Venezuela. **Upper**. Tropical thorn woodland off the road to Miraca 7 km west of the coastal road. View is to the south, and the open area in the foreground is a disturbed roadside. The blue and the green whiptails are sympatric in a similar area along this road 2 km east of this locality (see text and fig. 19). **Lower**. Mixed thorn woodland/very dry tropical forest habitat in the Monte Cano area west of Pueblo Nuevo. View is to the east/northeast from the Capuchino radar base.

of the blue and the green lizards were observed in July of several years. Burrows of green lizards were more conspicuous than those of blue ones because of the open habitats of the former; the blue lizards have burrows around the tangled roots of shrubs and trees in the thorn woodland community. Burrows of green lizards usually had a semiovoid opening up to 5 cm wide and were often on slight inclines with sparse vegetation; the burrows were acutely inclined and extended 20–40 cm into the ground. The green lizards also burrow under

or around suitable cover and sometimes utilize cover as shelter. At 16:00–18:00 hrs, several inactive ones were found under wooden planks in a garbage dump on the edge of Adicora; this site consisted of open sand hills with sparse vegetation. At another site 6 km south of Adicora, burrows of green lizards were along the edges of large concrete slabs associated with a dilapidated house on the coast. When disturbed, lizards often retreated under raised portions of the slabs or into burrows next to the slabs.

Green animals displayed tenacity in returning to the general burrow site. When burrows on hillsides in the Adicora dump were covered during the day, green animals returned to the area and excavated new ones later in the afternoon, or new burrows were observed the next morning.

In new piles of construction sand on an estate in Adicora at 18:00 hrs on 23 July, 1993, burrows of green lizards had a temperature of 31.7°C when the air temperature was 28.3°C; lizards uncovered from the burrows ran rapidly. A similar cooling lag of the ground relative to air temperature late in the day was observed in green lizard burrows at several other sites on the Paraguana Peninsula and also more recently by ALM in burrows of *Cnemidophorus gramivagus* on small, sandy hills in the llanos of Estado Apure, Venezuela. In all these cases, other areas near the burrows had lower ground temperatures than the burrow site selected by the lizard; it was often situated in a position of maximum solar radiation. The cooling lag may be significant to the lizards metabolism as it extends the length of the animals' daily high metabolic period without the necessity and perhaps risks of open basking.

Several other species of diurnal lizards were commonly observed in the same habitats with the blue or the green lizards. *Anolis onca* occurred in more open habitats with the green *Cnemidophorus*. *Ameiva bifrontata* was more commonly observed with the blue *Cnemidophorus* than with the green ones; Schall (1973) found *A. bifrontata* to be associated with forests on Aruba. Interspecific interactions involving this species and the two *Cnemidophorus* were not observed. The large peninsular *Ameiva ameiva* shared the same shaded habitats as the blue *Cnemidophorus* and was absent from the open areas occupied by the green ones.

Common names of both the blue and the green lizards on the Paraguana Peninsula vary (E. Wefer, personal commun.). Both are often simply referred to as "bisure." The green lizards are also called "lagarto verde" or "lagartija verda." Blue animals are often called "lagarto azul" or, by natives aware of the existence of the large, blue peninsular *Ameiva ameiva*, "lagartija azula," reserving the name "lagarto azul" for the *Ameiva*. An interesting legend pertaining to the blue *Cnemidophorus* exists among the inhabitants of the Monte Cano area; large males are said to attract snakes by putting a series of XXs on the ground in a ritualistic manner and then to kill the snakes so lured.

DIET

The blue and the green lizards differ in diet as well as habitat. Blue animals are insectivorous, as are most lizards, but the green animals are primarily herbivorous. Examination of 12 stomachs from freshly preserved field-collected blue lizards revealed exclusively arthropod material consisting of crickets, caterpillars, beetles and beetle larvae, and other unidentifiable insect parts. Eleven of 12 stomachs from green *Cnemidophorus*, however, contained plant material consisting of flower petals and parts, seeds, and achene type fruits; no identifiable green leaf or stem material was noted (one green lizard examined had an empty stomach). Of these eleven, six contained plant material exclusively and the five others a mixture of plant and animal material. In these five, plant material as a percentage of total material (in dry mass) ranged from 42.9 to 98.0% (mean = 75.2%, sd = 21.9%); two stomachs with a high percentage of plant matter (95.0%, 98.0%) contained small ants, which may have been incidental occupants of ingested flowers. Animal material in stomachs of green lizards consisted of ants, beetles, small wasps, crickets, beetle larvae, caterpillars, and small spiders. Two green females kept in captivity for three years readily ate and showed a preference for crickets, but they also accepted flowers from dandelion and clover plants. Schall observed *Cnemidophorus arubensis*, which consumes a primary diet of flowers and fruits

(Schall and Ressel, 1991), to show a preference for insects in captivity as well (personal commun.).

The facultative herbivory of the green *Cnemidophorus* of the Paraguana Peninsula not only parallels that of *C. arubensis* but also of *Cnemidophorus murinus* of Bonaire Island (Dearing, 1993), which is also close to the Paraguana Peninsula. Schall observed low insect abundance in the xeric habitats of *C. arubensis* (personal commun.), and this is also true of the open, xeric habitats of green lizards on the Paraguana Peninsula. Except during the short wet season, ground-dwelling insects are seen far less in these habitats than they are in the more closed habitats of the blue lizards. It is possible that the facultative herbivory of these three species in the Caribbean arid areas evolved in response to low insect availability.

Reproduction

Collections of the green *Cnemidophorus* during the Paraguanan dry season in July and during the wet season of late November allow an assessment of seasonality of reproduction. The small sample of blue females precluded such a comparison.

An ovarian follicular length of 3.0 mm was taken to be the criterion for reproductive maturity of females, as used by Dearing and Schall (1994) for *Cnemidophorus murinus*. The smallest green female that contained a follicle of 3.0 mm or more was 58 mm in snout-vent length (SVL) in a sample of 30 females. Six others under 58 mm SVL, two collected in November and four in July, had either follicles smaller than 3.0 mm or no measurable follicles at all. An approximate size at maturity of 60 mm SVL contrasts with 50 mm found by Leon and Cova (1973) in females of *Cnemidophorus lemniscatus* from Cumana, Venezuela.

The frequency of ovarian follicles and oviductal eggs in mature females suggests that the green animals have a long breeding season (fig. 22). Our data show a higher percentage of females with mature eggs in November than in July, but a contingency test of season and egg size category is nonsignificant ($\chi^2 = 3.82$; $P = .148$); nevertheless, the November sample is small. Schall (1973) considered the breeding

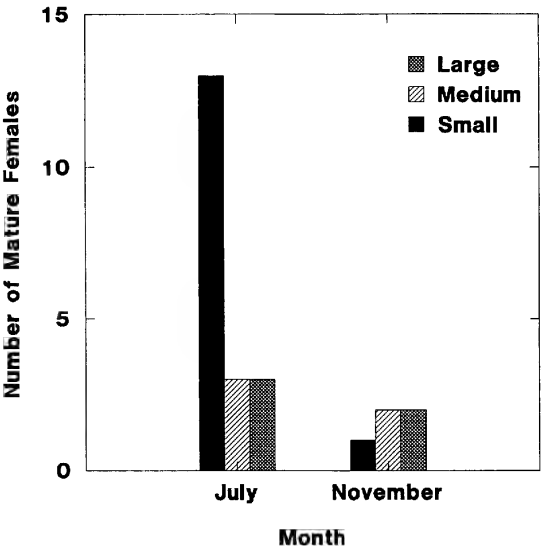

Fig. 22. Follicle size in green females (named *C. arenivagus* below) of the Paraguana Peninsula, in two seasons. Interpretation: small, yolking follicles < 3 mm in diameter; medium, follicles 3–10 mm in diameter; large, oviductal eggs, 10–15 mm long. Score is based on largest gamete or egg.

season of *Cnemidophorus* (probably the green species; see below) on nearby Aruba Island with a similar seasonal climate to be late November to late January. Del Conte (1972) found seasonally cyclic changes in testicular interstitial tissue of mature male *Cnemidophorus lemniscatus* in Maracaibo, Venezuela; the most intense interstitial activity corresponded to seasonal periods of greatest rainfall, temperature, and photoperiod. A trend toward seasonality in reproduction on the Paraguana Peninsula agrees with the suggestion of Fitch (1985) that reproduction in *C. lemniscatus* in seasonal climates is much retarded during dry seasons.

In the small sample of blue females, the smallest one with follicles of 3.0 mm or greater was 62 mm SVL, which is close to the size at maturity of the green females. Of eight female blue lizards, all three collected in November had large oviductal eggs while four of five from July had very small follicles and one a follicle of 5.5 mm in length.

The clutch size of green animals, determined by the number of large oviductal eggs, appears to be usually two and only occasionally one. Of the five animals depicted in figure 22 with large ova, four had two large

eggs (size range of ova, 12.5–16.0 mm in length), and only one was observed with one egg (15.0 mm); the mean clutch size was 1.8. Also, there appeared to be a very small size difference among ova within the females containing two; one female had ova of 16.0 and 15.5 mm, for example.

Clutch size of the blue lizards on the Paraguana Peninsula could be determined in only three females with large ova; two had two eggs and one had three (mean clutch size, 2.3). Oviductal eggs of these three (all collected in November) ranged from 10.9 to 11.2 mm in length. The largest ovum (14.5 mm in length) was in a blue-colored adult female from Miraca.

The clutch size observed in the peninsular *Cnemidophorus* is more similar to that observed in Venezuelan mainland *Cnemidophorus* than in nearby insular species. Leon and Cova (1973) recorded a clutch size of 2.4 for populations at Cumana, Venezuela, and Beebe (1945) observed *C. lemniscatus* at Kartabo, British Guiana and Carapito, Venezuela, to have two eggs per clutch. The nearby congener, *Cnemidophorus arubensis*, characteristically has one large egg per clutch, which Schall (1983) suggested might be related to its herbivory. The observation of the larger clutch size of nearby *Cnemidophorus* from the Paraguana Peninsula—only a short distance from Aruba—does not support this hypothesis because the green animals are herbivorous as well.

Finally, sexual size differences among mature *Cnemidophorus* from the Paraguana Peninsula yield a female/male ratio (the FMR of Fitch, 1981) of 91.0 for the green lizards and 84.3 for the blue ones. Both are higher than the female/male ratio of 79.4 reported for *C. lemniscatus* from Cumana, Venezuela (Fitch, 1981), and perhaps indicate less sexual selection for size differences on the Peninsula.

TAXONOMIC AND EVOLUTIONARY CONSIDERATIONS

The genetic, morphological, and ecological evidence we have presented indicates that the green lizards from the Paraguana Peninsula are highly distinctive from the sympatric blue ones and from *Cnemidophorus lemniscatus* populations to the east in the Guianan Region. Examination of museum specimens indicates that the green animal is not endemic to the Paraguana Peninsula and exists in other arid areas in mainland Falcon, Venezuela, as well as in nearby Colombia. These considerations, particularly the fixed differences in alleles present at more than six gene loci revealed by protein electrophoresis, and other differences discussed below, lead us to conclude that the green animals represent an undescribed species in the *C. lemniscatus* complex, which is named below.

The taxonomic status of the blue animal from the Paraguana Peninsula is less certain. The most obvious conclusion from our data is that it is much more closely related to *C. lemniscatus* of the Guianan Region than to the sympatric green lizards. Genetically, it differs from the Guianan *lemniscatus* at only one structural gene locus, and these lizards are similar morphologically in shape of the posterior margin of the central enlarged preanal shield, position of the nostril with respect to the nasal suture, shape of the frontonasal, number of finger and toe lamellae, number of gulars, number of granules around midbody, and other taxonomically important features. These characters also similarly distinguish both forms from the green *Cnemidophorus* of the Paraguana Peninsula.

Blue lizards differ from *Cnemidophorus lemniscatus* of the Guianan Region in several aspects of color pattern including the striking blue ground color of adult males and some females, the black ground color of adult females, a much lower number of granules between the paravertebral stripes, and the single, rather than split, vertebral stripe. The general similarities in scalation and biochemical genetics suggest that *C. lemniscatus* and the blue animals from northwestern Venezuela are conspecific, but the coloration differences appear to be conspicuous and consistent. Although a comprehensive study of geographic variation in *C. lemniscatus* was not an objective of the present paper, a cursory survey of several characters in lizards currently referred to *C. lemniscatus* from northern coastal areas of Venezuela and northeastern Colombia is suggestive (fig. 23). The vertebral stripe and number of granules between the paravertebral stripes (SPV) show a rather consistent pattern of variation that in-

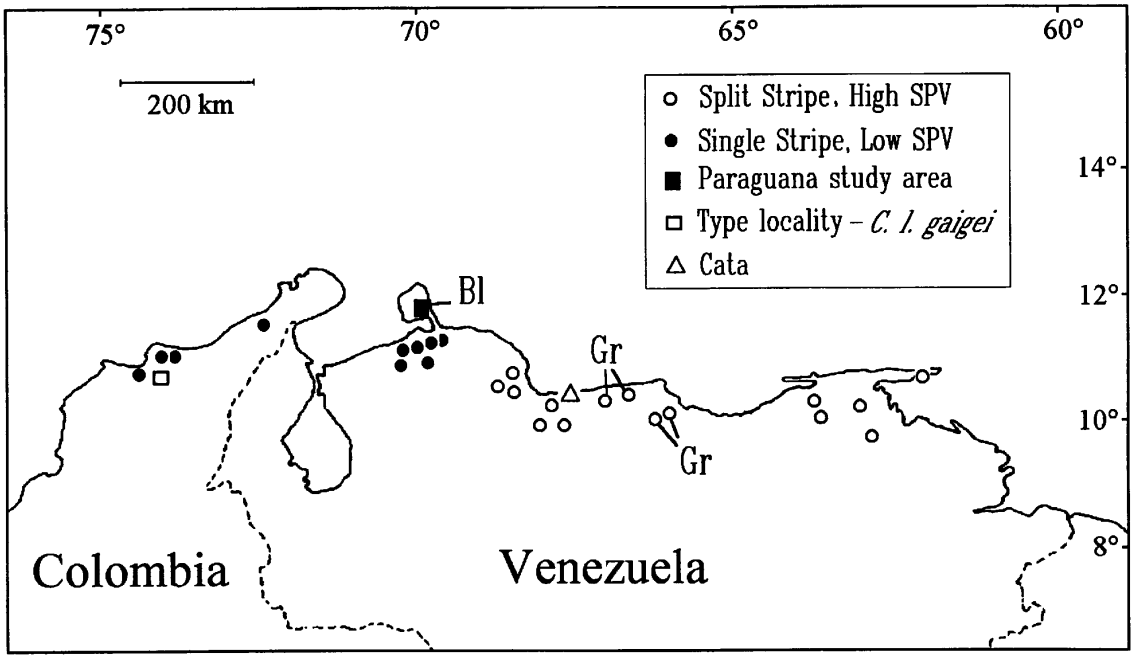

Fig. 23. Geographic variation in two features of color pattern (granules between paravertebral stripes [SPV] and condition of vertebral stripe [split or single]), in *Cnemidophorus lemniscatus* of northern Venezuela and northwestern Colombia. High versus low SPVs are within the ranges (with mean) of 15—28 (19) versus 8–19 (12), respectively. Colors (Bl, blue; Gr, green) corresponding to specified localities refer to predominant ground color in life as observed by Markezich; the Gr symbol does not refer to the green taxon of the Paraguana Peninsula, but to individuals of *C. lemniscatus* on the mainland with a largely green dorsum. The blue animals on the Paraguana Peninsula are recognized as a subspecies of *C. lemniscatus* below. Number of specimens for each locality is at least 3. The black rectangle on the Paraguana Peninsula represents the study area detailed in figure 19.

volves a split condition and high SPV, respectively, in eastern populations to as far west as the states of Aragua and Yaracuy, Venezuela, but a single stripe and low SPV in lizards from the northwestern arid areas of Venezuela and coastal Colombia. It thus appears that these two character states are not only typical of the blue animals from the Paraguana Peninsula but also of lizards from the northwestern coastal areas.

We do not know the taxonomic or adaptive significance of the split vertebral stripe or whether the geographic trend shown in figure 23 expresses more than sampling bias. Several populations confirmed by electrophoretic studies as *Cnemidophorus lemniscatus* from Guyana, Suriname, and Estado Bolivar, Venezuela (Cole and Dessauer, 1993, and the present study) show differences in where the light vertebral stripe splits. Guyanan and Venezuelan specimens have the stripe split on the neck or anterior shoulder region, while those from Suriname (see figs. 1 and 14) may display a split stripe down the entire length of the body. The split stripe appears to be at least partly correlated with geography.

Where else do populations of *Cnemidophorus lemniscatus* exhibit the striking blue color seen on animals from the Paraguana Peninsula? Without observing color in life, this is difficult to ascertain. Alcohol-stored specimens are subject to carotenoid pigment solubilization and/or oxidation, which tends to make originally green animals appear blue in storage (Test et al., 1966; also see comment below under subspecific description). Specimens from Cata, Estado Aragua, Venezuela, are intriguing in that they display a high number of granules between the paravertebral stripes, split vertebral stripe, and blue appearance in alcohol. Test et al. (1966) observed several bright blue *Cnemidophorus*

near the coast just west of Cata and considered this coloration very unusual for *C. lemniscatus*; they collected and observed most specimens of *C. lemniscatus* farther to the south at higher elevations in ecosystems different from those of arid lowland coastal localities. Their locality and Cata are in a narrow coastal strip with an arid climate and both thorn woodland and very dry tropical forest communities (MARNR, 1985)—ecological conditions similar to habitats of the blue lizards on the Paraguana Peninsula.

If the bright blue coloration is an adaptation to xeric woodland ecosystems, the blue *Cnemidophorus* probably had a broader historical distribution in northwestern Venezuela; paleobotanical evidence indicates that areas with arboreal vegetation at present had xeric herbaceous vegetation during the last glacial maximum, about 18,000 years ago (Haffer, 1987; Williams et al., 1993). As the area became more mesic about 10,000 years ago, arboreal vegetation appeared, and the xeric thorn woodland habitat of the blue lizard probably became fragmented and/or restricted to the drier coastal areas. As the animals from coastal Aragua have two characters (number of granules between the paravertebral stripes and condition of the vertebral light stripe) similar to *C. lemniscatus* to the east, it is possible that this is an area of intergradation between the blue animals of the peninsula and *C. l. lemniscatus*, but this remains to be demonstrated. In addition, adult males of *C. lemniscatus* in Suriname develop conspicuous blue coloration particularly during the breeding season (fig. 14A; note face, arms, and feet; also see Hoogmoed, 1973) as do males in Brazil (Avila-Pires, 1995: 701 [her striking color fig. 303]), so the seasonal development and comparative intensities of these blue colorations also need additional study.

Specimens of *Cnemidophorus lemniscatus* of the Santa Marta region, Departamento Magdalena, Colombia, were named *C. l. gaigei* by Ruthven (1915), who reported a large body size, fewer femoral pores, greater parietal scale width, and fewer parietal-postorbital granular scales. This taxon was relegated to the synonymy of *C. lemniscatus* by Burt (1931), who found it nondistinct after comparing it to other *C. lemniscatus*.

We have examined the holotype (UMMZ 45352) of *C. lemniscatus gaigei* and 16 paratypes and reached the same conclusion as Burt did concerning its lack of distinctiveness using Ruthven's characters. However, it may be distinctive with respect to some of the other diagnostic characters we have used (table 9; also see diagnoses below). In external morphology the holotype is clearly not conspecific with the green animals from the Paraguana Peninsula, and it is more similar to both *Cnemidophorus lemniscatus* from the east (Guianan Region) and the blue lizards of the Paraguana Peninsula; similar characters include shape of the frontonasal, shape of the posterior margin of the central enlarged preanal shield, position of the nostril with respect to the nasal suture, number of finger and toe lamellae, and number of gular scales and scales around midbody. The number of femoral pores in lizards of the *gaigei* type series is lower (mean in eight males, 38.7, in nine females, 39.0). In two features of color pattern, however, specimens of the type series are more similar to the blue animals from the Paraguana Peninsula than they are to the eastern populations of *Cnemidophorus lemniscatus*; they exhibit a low number of granules between the paravertebral stripes (mean, 14.1 in 17 specimens; compare to B and L animals in table 3) and normally a single vertebral stripe (but weakly split on the neck of two paratypes).

We have not seen live specimens from Departamento Magdalena, Colombia, but most preserved adult specimens have a light grayish-blue ground color. Ruthven (1915) stated that the color of the sides of the holotype was a bluish olive with orange patches behind the shoulder, very similar to that of live *Cnemidophorus lemniscatus* observed by one of us (ALM) several hundred kilometers to the east at Tacarigua, Estado Miranda, Venezuela. Also, the type specimen of *Cnemidophorus l. gaigei* has a profusion of light specks on the sides and on the dorsal surfaces of the thighs, in marked contrast to the larger light spots on these surfaces of the blue animals from the Paraguana Peninsula.

The type locality of *C. l. gaigei* is Fundacion, approximately 70 km S of Santa Marta (fig. 23), an area with dry forest communities and more precipitation than coastal areas to the north (Acevedo-Latorre, 1967). These ecolog-

ical conditions differ from those of the blue *Cnemidophorus* of the Paraguana Peninsula. Also, Ruthven (1915) did not comment on a striking blue dorsal color of any of the paratypes he collected nor did Muller (1971), in a comprehensive ecophysiological study of *Cnemidophorus lemniscatus* in and around the Santa Marta region. Several preserved specimens from the Santa Marta region other than the paratypes, however, and also several from an interior locality of the Guajira Peninsula, appear dark grayish blue in alcohol. The Santa Marta region is particularly complex with respect to its ecology, physiography, and microclimate (Ruthven, 1922). It is possible that various color-pattern morphs of *Cnemidophorus* are associated with different habitats in this region, as they are on the Paraguana Peninsula; additional detailed investigations are needed to resolve this, beginning with new fieldwork.

Cnemidophorus arubensis is among several species of lizards endemic to Aruba Island, only 30 km north of the Paraguana Peninsula. We lack karyotypic and electrophoretic data for *C. arubensis* but its morphology and color pattern are unlike that of the blue or the green animals from the Paraguana Peninsula, and it shows no clear affinity with either. *Cnemidophorus arubensis* has numerous, large light spots on the sides of the body and sometimes on the dorsum as well, and its color in life has been described as brownish green or bluish green (Lamerree, 1970; also compare fig. 5G of Wright, 1993, to figs. 13 and 14 here). Its most distinctive morphological character is an extremely high number of femoral pores ranging from 54 to 72. The frontonasal shape in our limited sample of *C. arubensis* is more similar to the blue animals than to the green ones but other characters (for example, shape of the posterior margin of the central enlarged preanal shield) show variation that spans the ranges in the blue and the green samples. Schall (1973) described its preferred microhabitat as open areas with large bushes, more similar to the microhabitats of the blue animals than to those of the green ones from the Paraguana Peninsula.

The Quaternary paleogeography of the Paraguana–Aruba Island area is worth reviewing with respect to the relationship of the insular *C. arubensis* to the *Cnemidophorus* of the Peninsula. During the last glacial maximum approximately 18,000 years before present, the Paraguana Peninsula probably was broadly connected with the Venezuelan mainland. The sea level was 120–150 m lower than it is now (Williams et al., 1993), and the water around Paraguana to the Guajira Peninsula to the west and to just southwest of Aruba Island is currently far shallower than 120 m (Shupe, 1992). However, a trench 200–247 m deep and approximately 5 km wide now exists near the southwestern Aruban shoreline. This trench may have been even deeper and wider, as it may have been partially filled by Recent siltation, as found for other offshore islands (Grismer, 1994). In any event, this trench probably separated Aruba Island from the Venezuelan mainland 18,000 years before the present. Thus, *Cnemidophorus arubensis* or its immediate ancestor may have been isolated from the mainland *Cnemidophorus* gene pools long before the last glacial maximum.

Knowledge of Quaternary geography and ecology gives little insight into the historical differentiation of the green *Cnemidophorus* of the arid areas in northwestern South America. Regardless of Pleistocene and Holocene sea-level changes (Williams et al., 1993), the strong northeastern/eastern trade winds likely created duneland and other open formations in the past, conditions to which this species is adapted. The considerable genetic and morphological differences between the green species and *C. lemniscatus*, as well as its facultative herbivory, suggests that it diverged from a *lemniscatus* or proto-*lemniscatus* ancestor earlier than the differentiation of the blue lizards in the arid areas. But this is speculative at best, as selective pressures associated with open arid areas could be intense, leading to a rapid rate of differentiation.

What about the taxonomic status of the blue animal from the Paraguana Peninsula? From all the data discussed above, we draw several conclusions: (1) it is not conspecific with the sympatric green animals on the Peninsula, nor is it *Cnemidophorus l. gaigei* or *C. arubensis*; (2) its color pattern differs from *Cnemidophorus lemniscatus* of the Guianan Region but its morphology and genetics are much more similar to these lizards than to any others; and (3) it appears to be a differentiated, lowland arid area form of (or

very closely related to) *Cnemidophorus lemniscatus*, associated with thorn woodland and very dry tropical forest habitats in northwestern Venezuela.

In ruling out a closer relationship between the blue taxon and the island forms than between the blue taxon and the mainland *C. lemniscatus*, we refer to the genetic evidence (see Evidence from Biochemical Genetics, above). The blue taxon is identical to *C. lemniscatus* at all except one or two of the 39 gene loci analyzed electrophoretically, depending on which populations are compared. Although no data are available for *C. arubensis*, Sites et al. (1990) showed that *C. murinus* differs from true *C. lemniscatus* (their cytotype D) at 17 of the loci they analyzed. We did not study all of the same loci as Sites et al., but we did test eight of those 17, so we would have detected differences between the blue taxon and *C. murinus* in at least six loci if *murinus* had been included in our samples.

Many systematists would regard the blue lizard as a new species because of the differences detected. However our knowledge of this taxon is limited and many questions need to be investigated, although its affinity with *C. lemniscatus* is clear. Consequently, we prefer to recognize the blue animals as a subspecies of *C. lemniscatus* to focus attention on the need for future research on the genetics, geographic variation, and ecology of this taxon and related populations. In particular, such research is necessary in mainland Venezuela and Colombia, with emphasis on coastal arid areas and populations that may (or may not) connect with the Central American lizards presently referred to *C. lemniscatus*. Indeed, if the blue taxon of northwestern Venezuela is not the local population of *C. lemniscatus*, what species is represented by the Central American lizards now referred to *C. lemniscatus*? The question of whether *Cnemidophorus l. gaigei* is a valid taxon merits further investigation also.

Results from the present study emphasize the importance of microgeographic and ecological data in studies of animals within the *C. lemniscatus* complex and perhaps of other teiids as well. The use of locality and morphology alone, although often nothing more is available, can easily mask the biotic complexities of tropical areas. Certainly, microgeography and ecology, coupled with genetic data, allow improved understanding of the evolution of these lizards and add to our understanding of the nature of Neotropical diversity in general.

DESCRIPTIONS OF THE NEW TAXA

Cnemidophorus arenivagus, new species

Figures 2, 4–7, 10, 13A, B, 15

HOLOTYPE: MCNG 1402 (field number and frozen tissue number ALM 5983), an adult male collected on 22 July 1993 by Allan L. Markezich in a desertified agricultural area 4 km N of Moruy (11°51′30″N, 69°58′W), Peninsula de Paraguana, Estado Falcon, Venezuela. Electrophoretic data are available for this specimen.

PARATYPES: VENEZUELA: The following are all from Estado Falcon, Peninsula de Paraguana or the associated Istmo de Medanos and were collected by A. L. Markezich and D. C. Taphorn in November–December, 1990: MCNG 1134 and 1135, 2 males from Istmo de Medanos, 17 km S of main peninsular body; MCNG 1142 and 1143, 2 males from E side of the coastal road 2.5 km S Adicora; MCNG 1155–1161, 7 males from E side of the coastal road 6 km S Adicora; MCNG 1182–1185, 1 male and 3 females from the dunes N of El Supi; MCNG 1190 and 1191, a male and female from 7 km E Las Piedras airport on the road to Jadacaquiva; MCNG 1211, a male from the entrance road to Las Piedras airport; MCNG 1162–1164, 2 males and a female from 1.7 km W of coast road (between Istmo and Adicora) on the road to Miraca (the road to Miraca intersects the coastal road approximately 10 km S Adicora); MCNG 1168, a female from 5 km W of coast road (between Istmo and Adicora) on the road to Miraca; and MCNG 1196–1202, 6 females and a male from the dunes 2 km N Las Tacques on the western peninsular coast. The following were collected by A. L. Markezich in July–August of 1989, 1991, 1992, and 1993: FMNH 242234, a male from 10 km NE Judibana; AMNH 142582, MCNG 1404–1407, MCNG 3002, MCZ 182142–182143, MHNLS 13234, ULABG 3864–3865, and USNM 507495–507496, 7 males and 6 females from E side of coastal road 6 km S Adicora; MCNG

1408, a male from 2 km S Miraca; FMNH 252724 and MCNG 1409—1412, 2 males and 3 females from the garbage dump just S of Adicora; AMNH 142587—142588, MCNG 1413–1422, TCWC 72859, and UMMZ 217167–217168, 7 males and 8 females from Adicora; and AMNH 142583–142586, MCNG 1423–1424, and MCNG 1426–1429, 3 males and 7 females from 4 km N Moruy (same locality as that of holotype).

Paratypes from the Peninsula de Paraguana or Istmo de Medanos also include: KU 223473 and MCNG 1430–1439, 8 males and 3 females from Adicora collected by E. Wefer in April, 1992; MCZ 155032, a male from Punta Cardon, and MCZ 155026–155031, all males from 4 km N Coro on the Istmo de Medanos road collected by M. Plotkin and R. Mittermeier in July, 1972; and FMNH 121072–121074, 3 females from Amuay Bay (west coast of Paraguana), collected by H. A. Beatty in September, 1960.

Paratypes from the mainland portion of Estado Falcon, Venezuela, include specimens in collections made by B. Patterson et al. in July, 1972: MCZ 133315, 133316, and 133340, all males from El Mamon; MCZ 133344, 133345, and 133347, two males and a female from 1 km SW Jebe; and MCZ 133319, 133320, 133334, 133335, 133337—133339, 1333711, and 133713, 2 males and 7 females from Urumaco and vicinity. M. Plotkin and R. Mittermeier collected the following mainland Falcon specimens in July, 1978: MCZ 155036–155038, 1 male and 2 females from 17 km W Coro, and MCZ 155035, a male from 38 km W Coro.

COLOMBIA: Departamento Guajira, FMNH 165389, and 165391–165395, 3 males and 3 females from Castilletes at the shore of the Gulf of Maracaibo, collected by H. LeNestour in September, 1960; and UMMZ 54842–54849, and 54851–54860, 9 males and 9 females from Riohacha, collected by A. G. Ruthven on July 18, 1920.

ETYMOLOGY: The specific appellation is a noun in apposition, meaning "wanderer of the sand." It refers to the typical duneland or desert scrub habitat of this species.

DIAGNOSIS: A species of the *Cnemidophorus lemniscatus* complex distinguished from all others by the following combination of characters: frontonasal usually quadrangular and rhomboidal with pointed sides; usually 2 frontoparietals; usually 5 parietals; usually 4 or 5 supraoculars on each side; if 5, additional supraocular normally a small accessory scale, about one-third to one-half size of first supraocular, within medial aspect of suture between first and second supraocular; nasal suture normally centered in nostril (in anterior-posterior direction); total (sum of left and right sides) fourth toe lamellae scales 57–74; total fourth finger lamellae scales 31–37; dorsal granular scales around midbody 81–105; abruptly enlarged mesoptychials; granular postantebrachials; central preanal shield often with acute angle on posterior margin; bisexual; males with one anal spur (shorter than in *C. gramivagus* and projecting more from side); adults with 4–6 (males) or 8–9 (females) longitudinal light stripes (including vertebral stripe); vertebral light stripe often absent or diffuse or subtle when present; 9–17 granules between paravertebral light stripes; numerous conspicuous light spots on legs; posterior thigh surfaces with light spots or spots fusing into irregular ovoid bands or blotches; faint light spots on arms; often conspicuous light spots laterally on body but lacking ventrolateral turquoise spots. Ground color of adults in life often vivid green with yellow or orange or brown lateral patches; head and arms often bright turquoise. Juveniles brown or light brown with 8–9 longitudinal light stripes and light spots conspicuous on arms and legs but absent on trunk. Ventral trunk surface of adults and juveniles light in appearance, with dark pigmentation absent. Maximum snout-vent length 93 mm; diploid number of 50 chromosomes, largest two being submetacentric to subtelocentric.

DESCRIPTION OF HOLOTYPE: This follows the format and wording of Hoogmoed's (1973: 267–269) description of *C. lemniscatus*, but is here based on *C. arenivagus*, MCNG 1402. Rostral pentagonal, visible from above, about as wide as deep. Nostril centered (anterior to posterior) and low in an obliquely divided nasal, the anterior parts forming a short median suture behind the rostral. Frontonasal rhomboidal. A pair of irregularly pentagonal prefrontals, forming a short median suture. Frontal hexagonal, longer than wide, wider anteriorly than posteriorly. A pair of irregularly pentagonal frontoparietals, forming a long median suture. Five irregularly shaped parietals in a

transverse series, the largest medial, and the two on each side small and subequal. Three large medial occipitals posterior to medial parietal, with 3 smaller ones to the right and 2 to the left of these. Back of head covered with small granules. Supraoculars 5/4 (left/right) with extra supraocular on left side (counted as supraocular number 5) a small wedge located medially between the first and second; the fifth/fourth (left/right) supraocular smallest; the second and third largest on each side. Supraoculars separated from the supraciliaries by generally one (anteriorly) or two (posteriorly) row(s) of granules, except first supraocular broadly contacts first supraciliary. Last supraocular separated from frontoparietals by a row of small scales (circumorbital semicircles, 7 scales on each side). Loreal large, more or less quadrangular with a posterior dorsal pointed process which contacts the first supraocular. Preocular absent. A row of 4 suboculars, forming a suborbital ridge; the anterior subocular more or less in a preocular position, deeper than long; the third longest. An irregular row of 4 enlarged postoculars with the dorsalmost and ventralmost the largest. Supraciliaries 5/6; the anterior 2 elongate and largest, the posterior ones quadrangular. A row of enlarged supratemporals. Enlarged scales in front of ear opening; central region of temple with small, round to oval granules. Ear opening large, surrounded by small scales forming smooth margin; external auditory meatus short, tympanum clearly visible. Seven large supralabials followed by small ones; the third largest, the sixth smallest; 5 supralabials to below center of eye. Lower eyelid with a semitransparent disc of 6/7 enlarged palpebrals. Pupil shape round.

Mental pentagonal with convex anterior margin. A pentagonal postmental. Five pairs of chinshields curving posteriad and dorsally to the infralabials; only anterior pair in contact at midline; the second through fourth pairs separated from the labials by 5 interlabial scales. Eight enlarged anterior infralabials, followed by small scales; third infralabial largest.

Gulars small, flat, rounded, juxtaposed, noticeably larger in the anterior part of throat, smaller in posterior part, which starts at level of ears; 21 gulars bordering chinshields noticeably larger than adjacent ones. Mesoptychials in front of prepectoral fold abruptly enlarged, slightly imbricate, smooth. Scales on nape and side of neck similar to dorsal and lateral body scales.

Dorsal and lateral scales granular, in transverse and indistinct oblique rows. Ventrals large, rectangular, wider than long, imbricate, smooth, in eight longitudinal and in 29 transverse rows (shoulder to hip); the anterior rows in midventral area interrupted by a small triangular area of smaller scales. Total number of dorsal granules around midbody 94. Preanal area with three enlarged, smooth, juxtaposed shields and smaller scales; two posterior shields subequal and semicircular with anteromedial flat sides bordering the enlarged central shield; central shield triangular with rounded anterior edge and pointed posterior one; angle at posterior apex is 82°. One anal spur on each side; each broad at base and tapered abruptly at about two-thirds distance to apex.

Femoral pores 20/20; two in preanal position on each side; each pore usually surrounded by three small scales (medial one usually largest in ring). Midventrally, 3 scales separate the femoral pore series of each side.

Scales on tail large, rectangular, obliquely keeled, slightly mucronate; imbricate, in transverse rows; keels forming longitudinal ridges. Scales under tail similar but narrower. Tail round in cross section.

Scales, on upper and posterior surfaces of upper arm (in live body position), on anterior and medial surfaces of forearm, on anterior and lower surfaces of thighs, and on lower surface of lower legs large, smooth, more or less hexagonal, imbricate; scales on lower and anterior surfaces of upper arm, on posterior and lateral surfaces of forearm, on posterior and upper surfaces of thighs, and on upper surface of lower legs small, ganular, juxtaposed (postantebrachials granular). Fourth finger lamellae number 18/17. Fourth toe lamellae number 32/32, usually single but divided under articulations. Four triangular, strongly enlarged and tubercular scales under third toe, proximally. Fingers and toes compressed. Palms and soles with small, irregular, juxtaposed, conical scales. Upper surfaces of hands and feet with large, imbricate flat scales.

In preservative (70% ethanol) for approximately two years after death, back and sides with four narrow, continuous grayish cream stripes, two in paravertebral and two in dor-

solateral (or first lateral) position; also a broad, diffuse, vertebral stripe. There are four brown stripes, two narrowly and laterally edging the vertebral light stripe and medially bordering the paravertebral stripes and two broad, darker brown ones in dorsolateral position below the paravertebral light and above the first lateral light stripes. Vertebral light and paravertebral dark stripes arise on the occipital area, are sharply defined on the neck and become diffuse and poorly defined anterior to the shoulder area, and continue onto the tail base for a short distance. Paravertebral light and dorsolateral dark stripes begin on lateral parietal area on each side and continue down trunk, ending a short distance down the proximal tail surface. First lateral light stripes are bordered sharply above by dorsolateral dark stripes, and begin on posterior superciliary area, continue down trunk, and end on proximal tail surface; they are then gradually represented on tail by a longitudinal series of scales with progressively smaller white tips, which vanish at end of proximal one-fifth tail length. Lateral trunk area light grayish blue, with second lateral light stripes represented by an unconnected series of grayish blue spots anteriorly and a short, continuous stripe to the groin; below this stripe are small, light grayish blue spots.

Dorsal head shields predominantly a dark blue gray, lateral head surfaces a lighter blue with diffuse, irregular, cream spots on the loreal and anterior suboculars; postorbital area a more vivid blue. The rostrum and large anterior supralabials edged above with light blue and below with cream; a light blue irregular spot on anteroventral temporal areas. Mental and first infralabial cream; other large infralabials cream with faint light blue mottling.

Arms above bluish gray with granules containing few light bluish gray spots; legs brownish gray above and dark blue anteriorly with bold creamish yellow spots associated with the granules; posterior thigh with a lower row of 3 light cream spots and one medial spot that continues as a short stripe onto the first few scales of tail base; upper surfaces of hands and feet light brown. Tail dark greenish blue dorsally and dorsolaterally; lower lateral sides light blue; ventral surface cream.

Ventral surfaces of trunk, head, and limbs predominantly cream and featureless; lateral gular area at level of ear with faint bluish wash; scales in first row of ventrals on each side either light bluish cream or darker bluish-gray, with light bluish cream forming spots on some; very slight blue wash on outer rows of ventrals.

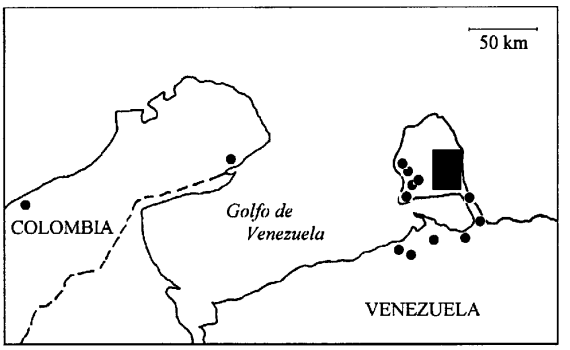

Fig. 24. Geographical distribution of *Cnemidophorus arenivagus*. The black rectangle on the Paraguana Peninsula represents the study area detailed in figure 19. This species apparently occurs on Aruba Island also, 30 km north of the Paraguana Peninsula (see Comments under the description of the species).

Fieldnotes and photographs indicate that the color of the holotype in life differed significantly from the above description. In life, lateral trunk surfaces predominantly green, with light yellowish green sides anteriorly and darker green posteriorly; light body stripes, as well as leg and arm spots, faint yellow; anterior lateral trunk spots bright green, posterior trunk spots light green. Vertebral area, except for the neck region, light brown; dorsolateral dark stripe darker brown than vertebral area with scales edged with black posteriorly. Anterior arm surfaces and first two fingers light turquoise, anterior femoral surface bright green, granular areas of arms light brown, of legs dark brown. Tail brown above with light turquoise on lower sides. Head mainly brown above with some greenish wash on the frontonasal and upper rostral and nasal surfaces; lateral supraorbital, postorbital, and suborbital surfaces green; spotting on loreal and temporal region light turquoise. Ventral throat, lateral two rows of ventrals on trunk, and edge of ventral tail surface light green; rest of ventral surfaces cream and featureless.

Snout-vent length 71 mm; tail 183 mm.

Hind limb approximately twice as long as arm. When laid along the body, there is considerable overlap of arm and hind limb.

DISTRIBUTION: The range includes the Peninsula de Paraguana and adjacent northern arid areas of the mainland portion of Estado Falcon, Venezuela, and the Guajira Peninsula, Departamento Guajira, Colombia (fig. 24). The species is associated with open sand dunes, desert, and desert scrub habitats.

VARIATION IN THE TYPE SERIES: In this paper we documented (above) variation in a large series of *Cnemidophorus arenivagus*, referred to as the green (or G) animals, from the Paraguana Peninsula. Paratypes from other areas depart little from these in most aspects of scalation and color pattern in alcohol. Nineteen specimens from proximal localities on mainland Falcon, south of the Paraguana Peninsula, exhibit a slightly higher number of femoral pores (mean = 44.1 in 9 males, 43.8 in 10 females) and scales around midbody (mean = 97.9 in males, 92.1 in females) than the population on the Paraguana Peninsula (table 3). Also, 52% of the mainland specimens have additional supraoculars compared to 42% from the Peninsula.

Seventeen paratypes from the Riohacha area of the Guajira Peninsula in Colombia exhibit a slightly higher number of granules between the paravertebral stripes (SPV) (mean = 13.6), a lower number of scales around midbody (SAB) (means, 87.5 in 8 males and 86.3 in 9 females), and a correspondingly higher SPV/SAB ratio (mean = 0.157) than the specimens from Paraguana. The number of toe lamellae is somewhat lower in the Guajira animals (mean = 62.5). Also, 62% of these have additional supraoculars. All other features of scalation and color pattern in the mainland Falcon and Guajira series agree well with the other paratypes.

Sexual dimorphism in characters dimorphic in Paraguanan populations was examined in these two populations as well; size was excluded because at least half of the individuals in each of these populations were juveniles. Both populations exhibited strong dimorphism in number of granules around midbody, and the Riohacha animals exhibited it in number of gulars as well; in each of these characters, males had higher values than females. There was not an apparent difference in number of femoral pores in males and females, but sample sizes were considerably smaller than the series from the Paraguana Peninsula.

COMMENTS: While *Cnemidophorus arubensis* occurs on most of Aruba Island and is quite common in some areas, Lammeree (1970) and Schall (1973) reported a small, local population of what they considered to be *Cnemidophorus lemniscatus* in the St. Nicolas area. Schalls observations indicated the absence of natural hybridization between these lizards and sympatric *C. arubensis* and consequently he supported specific status for the latter, which previously was considered a subspecies of *Cnemidophorus lemniscatus* by some authors. No specimens from St. Nicolas were available for us to examine, but Schalls descriptions of color pattern and habitat preferences as well as a photograph of one specimen in Lammeree (1970) strongly suggest that the population they referred to as *C. lemniscatus* is *C. arenivagus*. Consequently, Schalls observations on Aruba may be reinterpreted as the absence of hybridization between *C. arubensis* and *C. arenivagus*. Despite this, the isolation of *Cnemidophorus arubensis* and its obvious morphological and color-pattern differences from the nearby Paraguanan *C. lemniscatus* (see previous comments) are consistent with continuing specific rather than subspecific status for *C. arubensis*.

Cnemidophorus arenivagus exemplifies the difficulties in analyzing the systematics of whiptail lizards in South America, particularly concerning cryptic species that are best sorted out with genetic techniques. The specimen selected by Wright (1993: 39, his fig. 5E) to represent *C. lemniscatus* appears to be an example of *C. arenivagus*. Consequently, *Cnemidophorus lemniscatus* does not appear to be illustrated in Wright's review of the genus.

Cnemidophorus lemniscatus splendidus, new subspecies

Figures 2, 4–7, 10, 13C, 14C, 15

HOLOTYPE: MCNG 1403 (field number and frozen tissue number ALM 5963), an adult male collected on 22 July 1993 by Allan L. Markezich in a tropical thorn woodland community on a ranch 2 km S of Miraca (locality

coordinates 11°52′N, 69°52′30″W), Peninsula de Paraguana, Estado Falcon, Venezuela. Karyotypic and electrophoretic data are available for this specimen.

PARATYPES: VENEZUELA: The following are all from Estado Falcon, Peninsula de Paraguana, and were collected by A. L. Markezich and D. C. Taphorn in November–December, 1990: MCNG 1144–1145 and MCNG 1181, 2 males and a female from, Aguaque, "Casa Colonial," off road to El Vinculo; MCNG 1139–1141, 2 males and a female from Monte Cano, vicinity of Capuchino radar base; MCNG 1207, a female from Monte Cano, northwestern edge; MCNG 1165–1167, 2 males and a female from 3 km W of coastal road (between Istmo and Adicora) on the road to Miraca; MCNG 1169, a male from the same road but 5 km W of coastal road; and MCNG 1171, a male from same road but 8 km west of coastal road. One male was collected on 10 July, 1989, by A. L. Markezich: FMNH 242236 from Monte Cano, vicinity of Capuchino radar base. The following were collected by A. L. Markezich on July 20–25, 1993: AMNH 142591, 142593–142594, and 142596, MCNG 1440–1444, and USNM 507497–507498, 8 males and 3 females from 2 km SW San Jose de Cocodite, near El Pizarral; FMNH 252723, MCNG 1446—1449, MHNLS 13235, ULABG 3866, and UMMZ 217169, 7 males and 1 female from Aguaque, "Casa Colonial", off road to El Vinculo; AMNH 142590, 142592, and AMNH 142595, and MCNG 1450, 3 males and one female from 2 km S Miraca near El Pizarral; AMNH 142589, a male from Monte Cano, vicinity of Capuchino radar base; and MCNG 3001, a male from 1 km S of road bordering south edge of Monte Cano, in longitudinal alignment with Capuchino radar base.

The following were collected on the Paraguana Peninsula by M. J. Plotkin and R. A. Mittermeier in July, 1978: MCZ 155019–155023, 3 males and 2 females from the slope of Cerro Santa Ana; and MCZ 155024–155025, 2 males from 1 km S Pueblo Nuevo.

ETYMOLOGY: The subspecific name, *splendidus*, an adjective, refers to "magnificent" or "showy" and alludes to the striking brilliant blue ground color of adult males and some females.

DIAGNOSIS: A subspecies of *Cnemidophorus lemniscatus* distinguished from all others by the following combination of characters: femoral pores 41–53 (males), 39–47 (females); granules between paravertebral stripes (SPV) 8–19, normally 11–15; granules around midbody (SAB) 95–118 (males), 85–110 (females); SPV/SAB ratio 0.071–0.171; vertebral light stripe bold and single or absent at midbody. Ground color of adult males and some adult females in life a brilliant royal blue on most surfaces with 1–5 longitudinal light stripes (males) or 3–9 (females); vertebral and paravertebral light stripes, if present, often light tan or green; vertebral and paravertebral areas often with a blue or dark green wash in large males, obfuscating striping pattern; other light stripes blue, lighter than ground color, in blue individuals; all stripes light tan or yellow in some females with a black or dark brown ground color; dorsal thigh spots often tan or yellow in all; posterior thigh spots generally distinct and not forming lines or irregular blotches; often small light blue spots, 1–3 granules long, laterally on body in blue individuals, more conspicuous in males than females; females usually with bright turquoise ventrolateral spots often on first row of ventrals; both sexes occasionally with orange or orangish tan lateral patches on lateral trunk area. Juveniles with 8—9 longitudinal light stripes on a black or dark brown ground color with conspicuous light cream or tan spots on arms and legs but absent from trunk. Maximum snout-vent length 80 mm; diploid number of 50 chromosomes, largest pair being submetacentric to subtelocentric.

DESCRIPTION OF HOLOTYPE: This follows the format and wording of Hoogmoed's (1973: 267–269) description of *C. lemniscatus*, but is here based on *C. l. splendidus*, MCNG 1403. Rostral pentagonal, visible from above, about as wide as deep. Nostril somewhat anterior and low in an obliquely divided nasal, the anterior parts forming a short median suture behind the rostral. An octagonal frontonasal with a posterior acute and anterior obtuse shape. A pair of irregularly pentagonal prefrontals, forming a short median suture. Frontal hexagonal, longer than wide, wider anteriorly than posteriorly. A pair of irregularly pentagonal frontoparie-

tals, forming a long median suture. Five irregularly shaped parietals in a transverse series, the largest three medial and subequal, the two lateral ones smaller and subequal. Two large medial occipitals posterior to medial parietal, with 3 smaller ones to the right and 2 to the left of these; small granular scale in anteriormost suture between the two medial occipitals. Back of head covered with small granules. Supraoculars 4 with the fourth smallest and second and third largest on each side. Supraoculars separated from the supraciliaries by generally 1 (anteriorly) or 2 (posteriorly) row(s) of granules, except first supraocular broadly contacts first supraciliary. Last supraocular separated from frontoparietals by 1 (anteriorly) to 4 rows of small scales (circumorbital semicircles, 8/6, left/right). Loreal large, more or less quadrangular with a posterior dorsal pointed process that contacts the first supraocular. Preocular absent. A row of 4 suboculars, forming a suborbital ridge; the anterior subocular more or less in a preocular position, deeper than long; the third longest. An irregular row of 5 enlarged postoculars with the dorsalmost and ventralmost the largest. Supraciliaries 7/6; the anterior 2 elongate and largest, the posterior ones quadrangular. A row of enlarged supratemporals. Enlarged scales in front of ear opening; central region of temple with small, round to oval granules. Ear opening large, surrounded by small scales forming smooth margin; external auditory meatus short, tympanum clearly visible. Five large supralabials followed by small ones; the third largest, the fifth smallest; 5 supralabials to below center of eye. Lower eyelid with a semitransparent disc of 6 enlarged palpebrals. Pupil shape round.

Mental pentagonal with convex anterior margin. A pentagonal postmental. Five pairs of chinshields curving posteriad and dorsally to the infralabials; only anterior pair in contact at midline; the second through fourth pairs separated from the labials by 7 interlabial scales. Eight enlarged anterior infralabials, followed by small scales; third infralabial largest.

Gulars small, flat, rounded, juxtaposed, noticeably larger in anterior part of throat, smaller in posterior part, which starts at level of ears; 27 gulars bordering chinshields noticeably larger than adjacent ones. Mesoptychials in front of prepectoral fold abruptly enlarged, slightly imbricate, smooth. Scales on nape and side of neck similar to dorsal and lateral body scales.

Dorsal and lateral scales granular, in transverse and indistinct oblique rows. Ventrals large, rectangular, wider than long, imbricate, smooth, in 8 longitudinal and 29 transverse rows (shoulder to hip); the anterior rows in midventral area interrupted by a small triangular area of smaller scales. Total number of dorsal granules around midbody (SAB) 102, dorsal granules between paravertebral light stripes (SPV) 14; SPV/SAB = 0.137. Preanal area with 3 enlarged, smooth, juxtaposed shields and smaller scales; 2 posterior shields subequal and semicircular with anteromedial flat sides bordering enlarged central shield; central shield triangular with rounded anterior edge and pointed posterior one; angle at posterior apex, 128°. One anal spur on each side; each broad at base and tapered abruptly at about two-thirds distance to apex.

Femoral pores 23/24; 2 in preanal position on each side; each pore usually surrounded by 3 small scales (medial one usually largest in ring). Midventrally, 2 scales separate femoral pore series of each side.

Scales on tail large, rectangular, obliquely keeled, slightly mucronate; imbricate, in transverse rows; keels forming longitudinal ridges. Scales under tail similar but narrower. Tail round in cross section.

Scales, on upper and posterior surfaces of upper arm (in live body position), on anterior and medial surfaces of forearm, on anterior and lower surfaces of thighs, and on lower surface of lower legs large, smooth, more or less hexagonal, imbricate; scales on lower and anterior surfaces of upper arm, on posterior and lateral surfaces of forearm, on posterior and upper surfaces of thighs, and on upper surface of lower legs small, granular, juxtaposed (postantebrachials granular). Fourth finger lamellae number 15/16. Fourth toe lamellae number 27/26, usually single but divided under articulations. Three triangular, strongly enlarged and tubercular scales under third toe, proximally. Fingers and toes compressed. Palms and soles with small, irregular, juxtaposed, conical scales. Upper surfaces of hands and feet with large, imbricate flat scales.

In preservative (70% ethanol) for approximately 3 years after death, back with 3 narrow, continuous light cream stripes, 1 in vertebral and 2 in paravertebral position. Four black stripes, 2 narrowly and laterally edging vertebral light stripe and medially bordering paravertebral stripes and 2 broad, black ones in dorsolateral position below paravertebral light stripe. Vertebral and paravertebral stripes arise on occipital area, are sharply defined on neck and trunk and continue up to tail base; top of tail base with a subtriangular patch of cream lightly infused with darker cream. Dorsolateral black stripes begin on lateral parietal area on each side, continue down trunk and end a short distance down proximal tail surface. First lateral light stripes are light blue, thin and poorly defined, and intermittently connect roughly collinear spots; they begin on posterior superciliary area, continue down trunk, and also end on proximal tail surface, becoming gradually represented on tail by a longitudinal series of scales with progressively smaller white tips, which vanish at end of proximal one-fifth tail length. Lateral trunk area dark navy blue, with second lateral light stripes represented by collinear, unconnected light blue spots; below this stripe are small, light blue spots. Lateral trunk spots are 2–4 granules in diameter.

Dorsal and lateral head shields predominantly a dark gray blue with snout region a lighter blue and cream at tip of rostral. Poorly defined light blue spots on loreal, anterior suboculars, and supralabials. Mental and infralabials grayish blue, with large infralabials and chinshields with poorly defined light blue spotting. Gular region light blue with lighter blue spots.

Arms above dark blue with granular area containing a few light blue spots; legs dark blue above and anteriorly with bold creamish yellow spots associated with the granules; posterior thigh with 3 or 5 distinct light cream spots; upper surfaces of hands and feet light blue to brown. Tail dark blue dorsally and dorsolaterally; lower lateral and ventral surfaces light blue.

Ventral surfaces of trunk and limbs blue; first row of ventrals dark blue with intermittent light blue spots.

Fieldnotes and photographs indicate that the color of the holotype in life differed in a few respects from the above description. In life, head and lateral trunk and tail surfaces were predominantly a vivid dark royal blue, with contrasting creamish yellow vertebral and paravertebral stripes. Anterior arm surfaces and fingers blue like trunk, posterior surfaces tinged with black. Anterior leg surfaces dark blue like trunk, dorsal surfaces with bold creamish yellow spots on patches of black. Tail mainly blue, with obscure dorsal grayish brown striping continuing a short distance posteriorly from base and with small black patches posterior to thigh on dorsolateral surface. Undersurfaces were relatively featureless and light blue in life, with lighter blue gular spots.

Snout-vent length 80 mm; tail 91 mm, incomplete. Hind limb approximately twice as long as arm. When laid along the body, there is considerable overlap of arm and hind limb.

DISTRIBUTION: The subspecies is currently known from the thorn woodland and very dry tropical forest communities of the Peninsula de Paraguana (fig. 19), but it may occur in adjacent areas on mainland Venezuela (see Comments below).

VARIATION IN THE TYPE SERIES: We documented above several aspects of external morphological and color pattern variation in a large series of *Cnemidophorus lemniscatus splendidus*, referred to as the blue (or B) animals from the Paraguana Peninsula.

COMMENTS: *Cnemidophorus l. splendidus* is probably not endemic to the Paraguana Peninsula. Specimens from south of the peninsula in mainland Falcon, Venezuela (see fig. 23) may be this taxon. It may have a more extensive distribution in the northern coastal arid areas, correlated strongly with thorn woodland or very dry tropical forest communities in arid areas, such as in Cata, Estado Aragua, Venezuela, and on the Guajira Peninsula, Colombia, localities approximately 200 km east and west, respectively, of the Paraguana Peninsula (see above, Taxonomic and Evolutionary Considerations). We hesitate to designate specimens from these areas as paratypes because we know nothing of their color in life. Caution must be exercised in attempting to identify preserved specimens as *Cnemidophorus l. splendidus*. There is some fading of the dark blue of specimens of this subspecies in preservative (70% ethanol) to a slightly lighter blue than in life or to a grayish blue, but the general appearance is still relatively dark and lacks the

TABLE 9
Taxonomic Characters Useful in Identifying the *Cnemidophorus* Examined in the Present Study

Character	Taxon[b]		
	C. arenivagus	*C. l. splendidus*	*C. l. lemniscatus*
Shape of posterior apex of central preanal shield[a]	acute	obtuse	obtuse or split into two scales
Shape of frontonasal[a]	rhomboidal	hexagonal or octaganol	hexagonal or octaganol
Nostril in relation to nasal suture[a]	centered	anterior	anterior or far anterior
Ground color in life—adult[b] males	green or brown	blue	green or brown
Ground color in life—adult females	green or brown	black, blue, or dark brown	green or brown
Appearance of venter, preserved adult males	bluish white	dark blue	light blue
Ventrolateral turquoise spots, adult females in life	absent	present	present
Vertebral stripe[a]	single or absent	single or absent	split
SPV range (mean)[a]	9–17 (11.4)	8–19 (12.1)	15–28 (19.5)

[a] Also applies to juveniles.
[b] Adults are animals ≥ 60 mm SVL.

brilliance of life. However, deduction of color in life from preserved lizards is risky; green lizards often fade to a much lighter grayish blue, but dark green *Cnemidophorus l. lemniscatus* collected by one of us (ALM) in 1992 in Distrito Federal faded to dark grayish blue similar to that of *Cnemidophorus l. splendidus* after less than a year of storage in ethanol. Color in preservative is thus an unreliable indicator of subspecific identity in this case. We strongly encourage more observations on living specimens and their ecology to clarify the geographical distribution of *Cnemidophorus l. splendidus*, and we realize that its specific status may be changed in the future.

RAPID IDENTIFICATION OF SPECIMENS

Table 9 summarizes the salient features of color pattern and external morphology we found useful in identifying and distinguishing specimens of *Cnemidophorus arenivagus*, *Cnemidophorus l. lemniscatus*, and *Cnemidophorus l. splendidus*. With respect to the variation we found in the present study and the existence of cryptic species within the *lemniscatus* complex (Cole and Dessauer, 1993), we suggest that care be exercised in applying these criteria. We expect that criteria for identification will be modified as more is learned about variation in these and other closely related taxa. In addition, unfortunately, some species of the *Cnemidophorus lemniscatus* complex may prove to be best identified by examining the karyotype, selected structural gene products, and locality. *Cnemidophorus cryptus* and *C. pseudolemniscatus* appear to be such cryptic species and are very similar in characters of morphology and color pattern to those of *Cnemidophorus l. lemniscatus* in table 9.

ADDITIONAL NAMES AND RELEVANT TYPE SPECIMENS

In the course of reviewing published synonymies and relevant literature concerning *Cnemidophorus lemniscatus* (Burt, 1931; Peters and Donoso-Barros, 1970; Hoogmoed, 1973; Maslin and Secoy, 1986; Avila-Pires, 1995), we decided that several names and a few type specimens dating from one or two centuries ago need further discussion. We discuss first some nomina dubia, then the two type specimens of *Cnemidophorus scutata* Gray, 1845, and finally the lectotype of *Cnemidophorus lemniscatus* (Linnaeus, 1758).

Until about a decade ago most continental populations of whiptail lizards from Guatemala southward through Central America and northern South America (including a riparian and patchy distribution in Amazonia) were regarded as one widely distributed species, *Cnemidophorus lemniscatus*. Today we recognize two bisexual species and two unisexual species in addition to *C. lemniscatus* itself in this complex (including *C. gramivagus*, *C. arenivagus*, *C. cryptus*, and *C. pseudolemniscatus*), and future work may well result in elevating *C. l. splendidus* and other forms to recognition as species also. Some of these taxa are sufficiently similar to others as to be called cryptic species.

The process of understanding the taxa previously and presently masquerading under the name *C. lemniscatus* requires traditional work together with genetic analyses of specimens of known provenance. In many cases, this process is not conducive to resurrecting synonyms when names in addition to *C. lemniscatus* are needed, as the information available for many old names is inadequate for assigning them. For example, the following names are listed by Maslin and Secoy (1986) in the synonymy of *C. lemniscatus*: *Seps caerulescens* Laurenti, 1768; *Seps caeruleus* Laurenti, 1768; *Teius cyaneus* Merrem, 1820; and *Ameiva lineata* Gray, 1838. There are no useful type specimens or type localities associated with these names, nor are there descriptions or diagnoses sufficient for applying the names with reasonable certainty to any populations currently known in the *Cnemidophorus lemniscatus* complex. Consequently, these names must be set aside as nomina dubia.

The Types of *C. scutata*

Gray (1845: 21) named *Cnemidophorus scutata* on the basis of two unspecified specimens (one "male," one "female") of unstated provenance. Boulenger (1885: 364) synonymized *scutata* with *C. lemniscatus* and stated that the two types of *C. scutata* were from "S. America." We examined these types in order to see if they represent either the green taxon or the blue taxon named above, in which case the name *scutata* would apply.

The types (fig. 25) are BMNH 1946.8.8-61 and 1946.8.8-62 (formerly iii.19.A and iii.19.B, respectively). Both are males, despite Gray's mention of a female. According to a note in the bottle, dated 29 Sept. 1966, BMNH 1946.8.8-61 was going to be designated the lectotype of *C. scutata* by T. P. Maslin, but to our knowledge this was never done, and this was not mentioned by Maslin and Secoy (1986).

We present first the character state for BMNH 1946.8.8-61 (that of BMNH 1946.8.8-62 following in parentheses, if different), but for characters in which the two specimens are identical, only one state is given. Snout-vent length 77 mm (99 mm); tail length uncertain, broken and tied onto specimen (157 mm but with the posterior 103 mm regenerated); frontoparietals 2; supraoculars 5/4 (5/5); parietals 5; rows of ventrals at midbody 8; one anal spur on each side, short and projecting as in *C. lemniscatus*; postantebrachials granular; mesoptychials abruptly enlarged; nostril position somewhat anterior to nasal suture but not so far as being centered on nasal suture; preanal scales Type III, posterior and central ones similarly divided; gulars 24; frontonasal more or less hexagonal; circumorbital scales 4/4 (4/5); interlabial scales 3/3 (4/3); granules around midbody 112 (119); femoral pores 21/22 (22/22); interfemoral scales 2 (3); toe lamellae 31/32 (36/34); finger lamellae 17/17; vertebral light stripe split as in *C. l. lemniscatus*; scales between paravertebral light stripes 26 (27); light spots present on arms, legs, sides.

The types of *C. scutata* are clearly referable to *C. lemniscatus*, not to *C. arenivagus*. They differ from *C. l. splendidus* and are similar instead to *C. l. lemniscatus* in the following characters (see above and tables 3 and 9): condition of vertebral light stripe (conspicuously split in *scutata*); toe lamellae; scales between paravertebral light stripes; and the ratio of granules between the paravertebral stripes/scales around midbody. We conclude that the name *C. scutata* should remain as a junior synonym of *C. l. lemniscatus*.

The Lectotype of *C. lemniscatus*

When Cole and Dessauer (1993: 18) designated specimen NRM 126 as the lectotype of *Cnemidophorus lemniscatus* (see their fig.

Fig. 25. The type specimens of *Cnemidophorus scutata*, a junior synonym of *C. lemniscatus*. **A**. BMNH 1946.8.8-61, male, snout-vent length 77 mm. **B**. BMNH 1946.8.8-62, male, snout-vent length 99 mm.

9, p. 19), they had overlooked and were unaware of an earlier designation. Maslin and Secoy (1986: 25) had designated "ZMUU Linnaean Collection 15A" as the lectotype.

Dr. Lars Wallin of the Zoological Museum, Uppsala University, Sweden, provided photographs of the lectotype for us to reproduce here (figs. 26 and 27). He also confirmed (personal commun.) that this is a Linnaean specimen, although it is "quite small (67 mm totally), mutilated and badly preserved." The specimen appears to have become completely desiccated at some point. Nevertheless, it appears to be a *Cnemidophorus* with the anal spurs of a baby *C. lemniscatus*.

Fig. 26. Dorsal (**upper**) and lateral (**lower**) views of the lectotype of *Cnemidophorus lemniscatus*, ZMUU Linnaean Collection 15A.

SUMMARY AND CONCLUSIONS

1. The sympatric blue and the green *Cnemidophorus* of the Paraguana Peninsula in the northwestern Venezuelan arid lowlands were formerly considered to be one species, *Cnemidophorus lemniscatus*. We compared these lizards to each other and to true *C. lemniscatus* from Guayana, Suriname, and eastern Venezuela with respect to karyology, biochemical genetics, color pattern, scutellation, and ecological associations. The blue and the green animals represent two distinct, diploid, bisexual species.

2. The green lizards from the Paraguana Peninsula are an undescribed species, here named *Cnemidophorus arenivagus*. This species is known also from the arid areas of mainland Falcon, Venezuela, and the Guajira Peninsula, Colombia. Its habitat is open areas such as sand dunes and open desert communities. Like nearby insular congeners, it is a faculta-

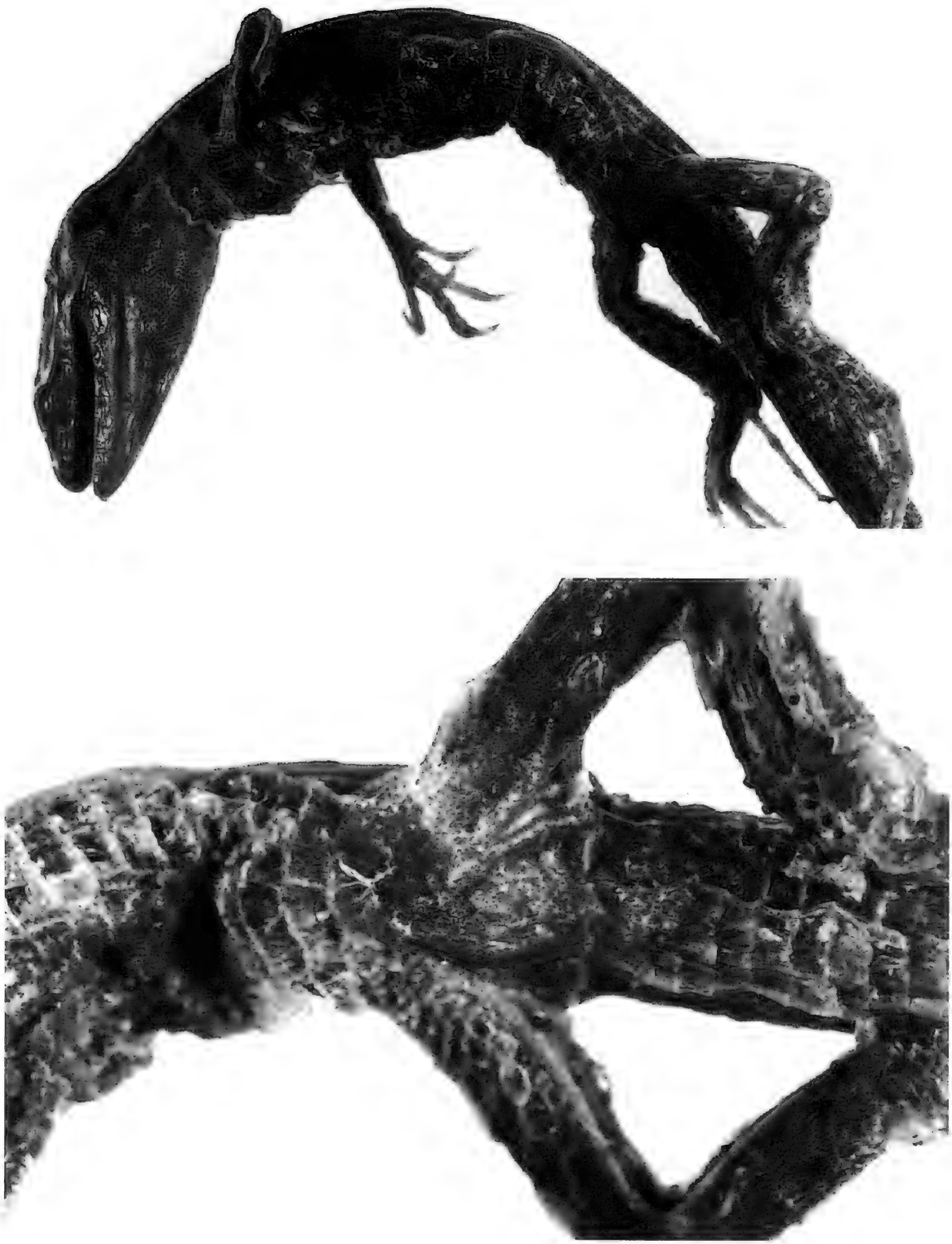

Fig. 27. Ventrolateral (**upper**) and ventral (preanal, **lower**) views of the lectotype of *Cnemidophorus lemniscatus*, ZMUU Linnaean Collection 15A.

tive herbivore, an adaptation that perhaps evolved in response to harsh environments with unpredictable insect availability.

3. The brilliant blue animals from the Paraguana Peninsula display a striking coloration that differs from the populations of *Cnemidophorus lemniscatus* from the Guianan Region, but they differ little in the 39 presumptive structural genes compared and other aspects of external morphology. Consequently, the blue taxon is here named a new subspecies, *Cnemidophorus lemniscatus splendidus*. Its ecological associations differ from those of *Cnemidophorus arenivagus* in that *splendidus* occurs in thorn woodland and very dry tropical forest communities and appears to be strictly carnivorous. It may occur in these ecological associations in other arid areas of northern Venezuela and adjacent Colombia and may have had a more extensive distribution during the last glacial maximum owing to greater aridity and more extensive xeric floral communities in northwestern Venezuela.

4. The two species of the Paraguana Peninsula are microgeographically allopatric or parapatric in most areas of the southeastern quadrant of the Peninsula. They are allotopic at several localities of sympatry where there are mosaic habitats as a result of human disturbance, and there is no evidence of hybridization. Structural characteristics of vegetation and degree of openness in the habitat appear to be important in habitat partitioning.

5. Both species, as well as *C. lemniscatus* from the Guianan Region to the east, exhibit sexual dimorphism in size as well as in several aspects of scalation.

6. Variation in color pattern of *Cnemidophorus arenivagus* and *Cnemidophorus l. splendidus* on the Paraguana Peninsula involves ontogenetic and sexual components. Males of each generally lose stripes with growth and acquire either their bright green or bright blue ground color. Adult females, on the other hand, usually retain their juvenile striped pattern to some degree but are dichromatic and can have a brown or black ground color. Alternatively, some adult females develop either the blue or the green ground color similar to that of their respective males.

7. Both species from the Paraguana Peninsula apparently have a normal clutch size of two eggs, and females attain sexual maturity at approximately 60 mm snout-vent length.

8. *Cnemidophorus lemniscatus gaigei* of the Santa Marta region of Departamento Magdalena, Colombia, is currently synonymized with *Cnemidophorus l. lemniscatus*. This is a *C. lemniscatus* that differs from *Cnemidophorus l. splendidus* in several aspects of color pattern and possibly in ecological associations. It may be found to be a distinct taxon when more information is available.

9. The relationship of *Cnemidophorus arubensis*, a species endemic to Aruba Island, to the nearby Paraguanan *Cnemidophorus arenivagus* and *C. l. splendidus* is presently obscure. Its color pattern and morphology as well as biogeographic considerations indicate that it is a distinct species rather than a subspecies. Work by others suggests that it does not hybridize with lizards that we identify as probably *C. arenivagus* at a locality where they are sympatric on Aruba island.

10. The present study emphasizes the importance of genetic, ecological, and microgeographic observations in studies of the *C. lemniscatus* complex.

11. Table 9 is presented for identifying the two new taxa described as well as *Cnemidophorus l. lemniscatus* from eastern Venezuela, Guyana, and Suriname.

12. The type specimens of *Cnemidophorus scutata* (a synonym of *C. lemniscatus*) are described, and the lectotype of *Cnemidophorus lemniscatus* is illustrated. The following names must be set aside as nomina dubia: *Seps caerulescens* Laurenti, 1768; *Seps caeruleus* Laurenti, 1768; *Teius cyaneus* Merrem, 1820; and *Ameiva lineata* Gray, 1838.

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APPENDIX
Specimens Examined

The specimens are referred to by their individual catalog numbers, and initials for their respective collections are as follows: AMNH (American Museum of Natural History); FMNH (Field Museum of Natural History); KU (University of Kansas, Museum of Natural History); MCNG (Museo de Ciencias Naturales, UNELLEZ, Guanare, Estado Portuguesa, Venezuela); MCZ (Museum of Comparative Zoology, Harvard University); MHNLS (Museo de Historia Natural, Sociedad de Ciencias Naturales La Salle, Caracas); TCWC (Texas Cooperative wildlife Collection, Texas A & M University); ULABG (Universidad de Los Andes, Instituto de Geografia, Merida, Venezuela); UMMZ (University of Michigan, Museum of Zoology); and USNM (United States National Museum of Natural History). The lowercase letters following the catalog numbers indicate the kind of data taken from each specimen, as follows: e, external morphology; k, karyotype; p, protein electrophoresis. An "e*" specifies those specimens used for analysis of external morphology and color pattern in comparing the blue and the green lizards from the Paraguana Peninsula and *Cnemidophorus lemniscatus* (see Evidence From Morphology: Comparisons Among the Blue and the Green Lizards from the Paraguana Peninsula and *C. lemniscatus*).

Cnemidophorus arenivagus

VENEZUELA: State of Falcon; Paraguana Peninsula; 4 km (linear) N Moruy (holotype, MCNG 1402, ALM 5983, e*, p; AMNH 142583–142585 e*, k, p; ALM 5968, e*, p; AMNH 142586 e*, p; MCNG 1423–1424, e*, p; MCNG 1426–1429, e*, p); Istmo de Medanos, 17 km S of main peninsular body (MCNG 1134–1135, e); 4 km N Coro on Istmo de Medanos road (MCZ 155026–155031, e); 2.5 km S Adicora off coastal road (MCNG 1142–1143, e*); E side of coastal road 6 km S Adicora (AMNH 142582, e*; MCNG 1155—1161, e*; MCNG 1404–1407, e*; MCNG 3002, e*; MCZ 182142–182143 e*; MHNLS 13234, e*; ULABG 3864–3865, e*; and USNM 507495–507496, e*); 1.7 km W of coastal road (between Istmo and Adicora) on the road to Miraca (MCNG 1162–1164, e*); 5 km W of coastal road (between Istmo and Adicora) off the road to Miraca (MCNG 1168, e*); Adicora (AMNH 142587–142588, e*, p; FMNH 252724, e*; KU 223473, e*; MCNG 1409—1422, e*; MCNG 1430–1439, e*; TCWC 72859, e*; UMMZ 217167–217168, e*); El Supi (MCNG 1182–1185, e*); 7 km E Las Piedras Airport on road to Jadacaquiva (MCNG 1190–1191, e); Las Piedras Airport (MCNG 1211, e); 2 km N Las Tacques (MCNG 1196—1202, e); 10 km (linear) NE Judibana (FMNH 242234, e); 2 km (linear) S Miraca (MCNG 1408, e*); Amuay Bay (FMNH 121072–121074, e). From state of Falcon, mainland localities; El Mamon (MCZ 133315–133316, e; MCZ 133340, e); 1 km SW Jebe (MCZ 133344–133345, e; 133347, e); Urumaco (MCZ 133319–133320, e; MCZ 133334–133345, e; MCZ 133337–133339, e; MCZ 133711, e; MCZ 133713, e); 17 km W Coro on road to Maracaibo (MCZ 155036–155038, e); and 38 km W Coro on road to Maracaibo (MCZ 155035, e). COLOMBIA: Departamento Guajira; Castilletes (FMNH 165389, e; FMNH 165391—165395, e); and Riohacha (UMMZ 54842–54849, e; UMMZ 54851–54860, e).

Cnemidophorus arubensis

ARUBA ISLAND: USNM 79323–79325, e; USNM 79327–79331, e; eastern edge of Seroe Colorado (town), USNM 266297, e; 0.5 km N of Salinja Cerba, USNM 266298, e; E of Oranjestad, Camacuri area, USNM 266299.

Cnemidophorus cryptus

VENEZUELA: State of Bolivar; Icabaru (AMNH 135089, p; AMNH 134231—134232, p; and AMNH 134234, p).

Cnemidophorus l. lemniscatus

GUYANA: northern Rupununi savanna; Yupukari (on the Rupununi River), 12 km

(linear) SW Karanambo (AMNH 138058–138062, e*, p; AMNH 138065–138069, e*, p; AMNH 138070–138077, e*; and AMNH 138082, e*); Karasabi village, 42 km (linear) NW Karanambo (AMNH 138099–138108, e*); Jouri, 33 km (linear) NW Karanambo (AMNH 138109–138110, e*). SURINAME: Marowijne District; Christiaankondre, near mouth of Marowijne River (AMNH 133292–133293, e*, k, p; AMNH 133294–133297, e*, p; AMNH 133298–133299, e*; AMNH 133300–133303, e*, k, p). VENEZUELA: State of Bolivar, San Ignacio de Yuruani (AMNH 134221, e*; AMNH 134222–134228, e*, p; AMNH 134229—134230, e*; AMNH 135091, e*, k, p; and AMNH 135092, e*, p). SOUTH AMERICA (BMNH 1946.8.8-61–1946.8.8-62).

Cnemidophorus l. splendidus

VENEZUELA: State of Falcon; Paraguana Peninsula; 2 km (linear) S Miraca (holotype, MCNG 1403, ALM 5963, e*, k, p; AMNH 142590, e*; AMNH 142592 and 142595, e*, p; MCNG 1450, e*); Aguaque, "Casa Colonial" (FMNH 252723, e*; MCNG 1144—1145, e*; MCNG 1181, e*; MCNG 1446–1449, e*; MHNLS 13235, e*; ULABG 3866, e*; UMMZ 217169, e*); Monte Cano, Capuchino (AMNH 142589, e*; FMNH 242236, e; MCNG 1139—1141, e*; MCNG 1207, e*; and MCNG 3001, e*); 3 km W of coastal road (between Istmo and Adicora) off the road to Miraca (MCNG 1165–1167, e*); 5 km W of coastal road (between Istmo and Adicora) off the road to Miraca (MCNG 1169, e*); 8 km W of coastal road (between Istmo and Adicora) off the road to Miraca (MCNG 1171, e*); 2 km (linear) SW San Jose de Cocodite, near El Pizarral (AMNH 142591, e*; AMNH 142593–142594, e*, k, p; AMNH 142596, e*, p; MCNG 1440–1442, e*; MCNG 1443–1444, e*, p; USNM 507497–507498, e*); Cerro Santa Ana (MCZ 155019–155023, e); and 1 km S Pueblo Nuevo (MCZ 155024–155025, e).

Cnemidophorus lemniscatus
(subspecies unassigned)

VENEZUELA: State of Anzoategui; near Carapa (USNM 80608–80609, e). State of Aragua; Cata (AMNH 99167, e; AMNH 99169, e; AMNH 99171, e; AMNH 99173, e; AMNH 99175, e; AMNH 99190, e; AMNH 99198, e; AMNH 99206-99208, e; AMNH 99212-99213, e; AMNH 99215, e; AMNH 99218, e; AMNH 99221, e; AMNH 99224, e; AMNH 99227, e; AMNH 99230, e; AMNH 99231, e); Rancho Grande, Island Point (UMMZ 137253, e); along Ocumare River road from Rancho Grande to Ocumare (UMMZ 124324, e; UMMZ 124326, e); Ocumare road, 1600-1700′ (UMMZ 124327, e; UMMZ 124329, e; UMMZ 124330 [2 specimens], e); Turiamo (UMMZ 124325 [2 specimens], e; UMMZ 124328, e). State of Carabobo; Laguna Valencia (AMNH 99277–99278, e). State of Falcon; Urumaco (MCZ 133314, e; MCZ 133317–133318, e; MCZ 133321–133333, e; MCZ 133336, e; MCZ 133338, e; MCZ 133709–133710, e; MCZ 133712, e); El Mamon (MCZ 133341–133342, e); 1 km SW Jebe (MCZ 133343–133347, e); Coro (MCZ 133349–133350, e); Punta Cardon (MCZ 155032, e); banks of Rio Sabaneta, 46 km W Coro on Coro-Maracaibo road (MCZ 155033–155034, e); Tucacas (UMMZ 55912, e; UMMZ 55921, e; UMMZ 55944, e). Distrito Federal (UMMZ 203981, e); Catia (ALM 8113). State of Monagas; Caripito (AMNH 57352–57356, e); 55 km SE Maturin (USNM 217100, e). State of Sucre; 9 km N Guiria (USNM 217102, e). State of Yaracuy; Palma Sola (UMMZ 55904, e; UMMZ 55906, e; UMMZ 55913, e; UMMZ 71464 [3 specimens], e); Rio Aroa (UMMZ 55910, e); Aroa (UMMZ 71463, e); Nirgua (UMMZ 55916, e); Rio Nirgua (UMMZ 55918, e; UMMZ 55941, e; UMMZ 55965, e). COLOMBIA: Departamento Magdalena; Fundacion (UMMZ 45352, holotype of *Cnemidophorus l. gaigei*, e; UMMZ 45327, e; UMMZ 45367, e); Mamatoca and Latigera (UMMZ 45329, e; UMMZ 45332, e; UMMZ 45320, e; UMMZ 45363, e; UMMZ 45335, e; UMMZ 45366, e; UMMZ 45370, e; UMMZ 45351, e; UMMZ 45339); Minca (UMMZ 45328, e; UMMZ 45347, e); Salamanca Coast (UMMZ 45334, e; UMMZ 45337, e); Tamocal River (UMMZ 45330, e).

Note added in proof: A report just published on herbivory in "*Cnemidophorus lemniscatus*" probably pertains to *Cnemidophorus arenivagus*. The lizards were seen eating flower petals of *Opuntia* on the Paraguana Peninsula (A. Mijares-Urrutia, B. Colvee, and A. Arends R., 1997, Herpetol. Rev. 28(2): 88).